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VENEZUELAN CAVE CRICKETS WITH VARIABLY REDUCED EYES*

by
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ABSTRACT

Light and electron photomicroscopy were used to study variability in eye regression of populations of a cavernicolous gryllid cricket from northern Venezuela. Statistical analysis suggests that there are two distinct types or subspecies each with a separate habitat preference. The microphthalmic type is probably better adapted to life in low-energy, deep-cave environments but is outcompeted in high-energy environments (e.g. guano beds) by the macrophthalmic type.

INTRODUCTION

During the 1973 British-Venezuelan Karst Research Expedition (Chapman and Checkley, 1981), a number of crickets, so far unidentified members of the family Gryllidae, were collected in caves of the Serrania de San Luis, Estado Falcón, Venezuela (Plate 1). These crickets were common in most caves explored by the expedition (Chapman, 1980). The populations in caves such as Camburales and Cuatro Vientos, which abound in nutritious bat guano, included a range of phenotypes from heavily pigmented, large-eyed forms (Plate 2), to microphthalmic, depigmented forms (Plate 3). However in caves such as La Madame and Guarataro, where energy input in the form of exogenous organic matter is low, only the microphthalmic, depigmented form was present. The wide range of phenotypes suggested either genetic polymorphism within an interbreeding population, or that more than one subspecies were represented and that they differed in their degrees of cave-adaptation. The most easily quantified variation between individual crickets is in the number of corneal lenses making up the surface of their compound eyes. It was therefore decided to study this single character as an indication of more general phenotypic variations.

METHOD

Rather than attempt a comparative study of crickets from all the caves in the Serrania, which would have proved immensely time consuming,

* Since this paper went to press, the crickets, originally examined by an expert in France, have been re-examined by Dr. T. H. Hubbell (Michigan) who suggests that the microphthalmic and macrophthalmic types belong to two distinct species within the gryllid subfamily Phalangopsinae.

examples from just two caves were studied. The caves were Camburales and Coy-Coy. In order to compare populations from a wide range of habitats, crickets were collected from the following regions of the caves:

(A) Coy-Coy Cave

Group CC1. From the two large seed beds closest to the entrance. Lying below currently occupied oilbird roosts, these sites receive a constant energy input in the form of regurgitated palm seeds and droppings and are therefore classed as 'high energy' sites.

Group CC2. From the cave floor surrounding a patch of wet mud, 560m. from the entrance. Occasional floods appear to introduce a little fresh mud which is assumed to have some organic content. This area is therefore classed as a 'low energy' site.

Group CC3. From an old dry seed bed 800m. from the entrance. This region of the cave is long-abandoned by oilbirds and with no apparent energy input. Whilst much organic material may remain in the crumbly brown seed remains, it is doubtful if this is in a form which can be used by crickets (nor any other arthropods judging by the low density of all arthropods in this region). This area is therefore classed as a 'very low energy' site.

(B) Camburales Cave

Group CA1. From a large area of mud, 50m. from the entrance. Though no bats roost in this area, it receives occasional droppings from bats passing into deeper portions of the cave, and is therefore classed as a 'low energy' site.

Group CA2. From the main chamber which has a sparse but permanent bat population and small scattered guano deposits, and is therefore classed as a 'high energy' site.

Group CA3. From teeming guano beds in the 'Bat Chamber' and 'Bat Sewer' which contain huge, densely-packed bat populations. This is classed as a 'very high energy' site.

All sites are in darkness, apart from a corner of the entrance seed bed in Coy-Coy which is dimly illuminated from the small, overhung entrance.

To avoid collecting bias, only those crickets taken in unbaited pitfall traps were studied.

The 84 crickets collected in Camburales and Coy-Coy caves were preserved in ethanol and subsequently studied at the University of Bristol. One eye of each cricket was photographed through a light microscope. The negatives were projected on to a screen and the corneal lenses were counted. This method was successful with specimens whose eyes were heavily pigmented, but the eyes of some specimens were depigmented to such an extent that it was impossible to discern individual lenses through the light microscope. After a number of staining techniques had been tried un-

Plate 1: A cricket from Cueva el Coy-Coy de Uria.

Plates 2 and 3: Crickets from Cueva de Camburales:

Plate 2: macrophthalmic type (c.200 corneal lenses per eye).

Plate 3: microphthalmic type (c.60 corneal lenses per eye).

successfully, the remaining specimens' eyes were photographed at low magnification under a scanning electron microscope. This proved successful.

Raw data were tabulated according to the sample group from which the specimens were obtained (see Appendix). From these data, using class intervals of 10, frequency histograms (Fig. 9) of numbers of corneal lenses per eye were constructed for each cave.

The Mann-Whitney U Test (see Siegel, 1965) was used to ascertain how the samples from different sites within each cave differ from each other. In this case the Null Hypothesis (H_o) is that the samples from different sites within the cave do not differ with respect to the numbers of corneal lenses in their eyes. The Alternative Hypothesis (H_i) is that such samples do differ in this respect. The level of significance was chosen at $=0.10$. Since H_i does not predict the direction of difference, the region of rejection is two-tailed.

RESULTS and DISCUSSION

Results of the Mann-Whitney U test were as follows:

Comparing CC1 with CC2, CC2 with CC3, CA1 with CA2, and CA2 with CA3, in each case H_o is valid at $=0.10$.

For the two remaining pairs, the probabilities of occurrence under H_o are: CC1 with CC3 $=0.072$, CA1 with CA3 $=0.00046$.

Thus there is a just significant difference in number of corneal lenses (or corneal lens count, – c.l.c. for short) between the crickets from the energy-rich active seed beds and those from the old, dry seed bed in Coy-Coy, and a highly significant difference between the crickets from the energy-poor entrance region and those from the energy-rich 'Bat Chamber' and 'Bat Sewer' in Camburales cave.

The c.l.c. frequency histograms (Fig. 9) show polymodality. This is interpreted as follows:

(1) More than one genetic morph or subspecies is represented in the samples.

(2) A single morph or subspecies characterized by a range of c.l.c.s from 50 to about 90, with a mode of 60–70, is present in both caves. This will from now on be referred to as the 'microphthalmic type'.

(3) A 'macrophthalmic type' occurs in Camburales and infrequently in the entrance region of Coy-Coy. This 'type' has a range of c.l.c.s. from around 100 to 230, with no dominant mode.

The way in which the two types of crickets are distributed within the caves provides circumstantial evidence concerning possible differences in their metabolic functioning and evolutionary histories. The mean c.l.c. of crickets inhabiting the energy-rich Bat Chamber and Bat Sewer in Camburales (see CA3, Table 3) is close to the mean c.l.c. of the macrophthalmic type. In contrast to this, the mean c.l.c.s of populations in low energy regions of both caves are very close to the microphthalmic modal c.l.c. In fact both cricket types are found in regions of high energy

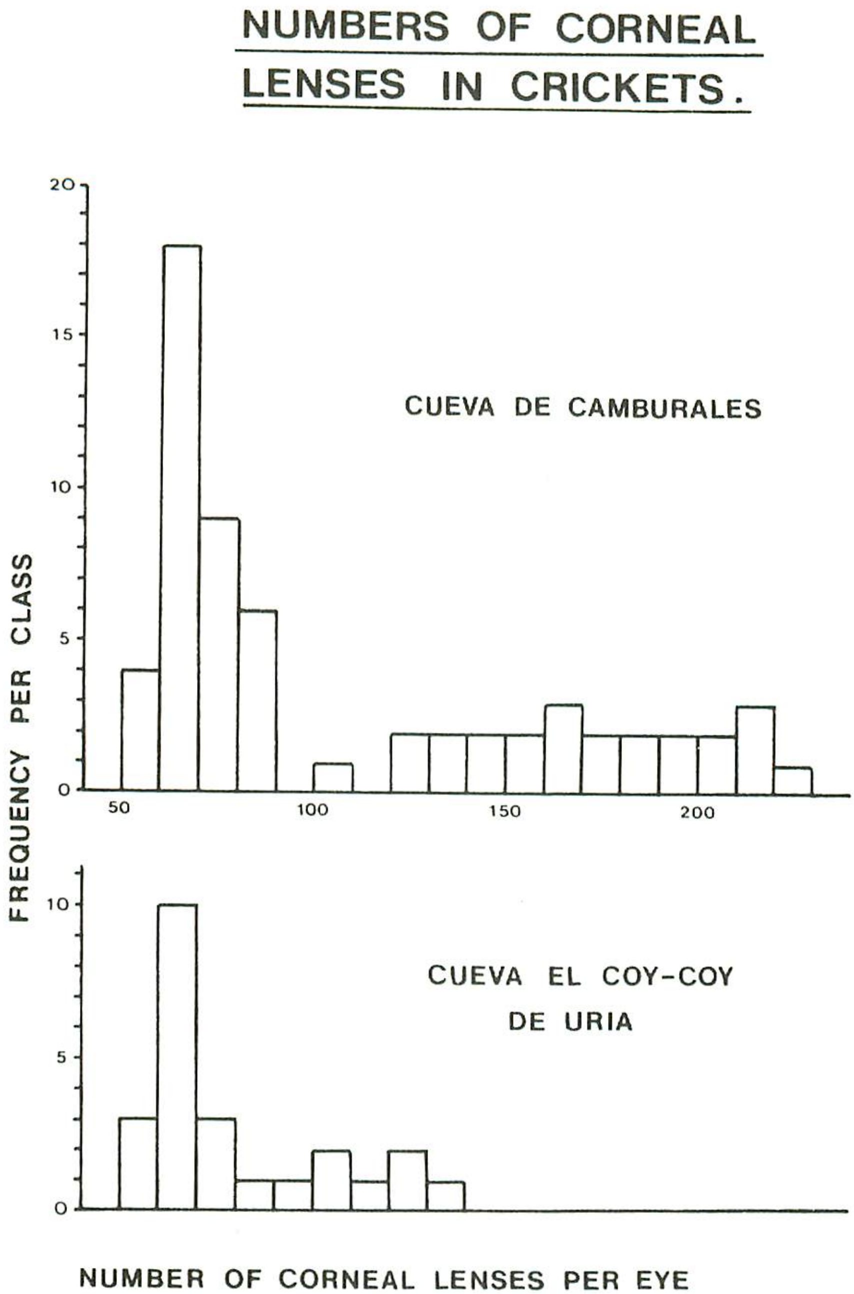

Fig. 9: Corneal lens count

input (the macrophthalmic type being the more numerous), producing large standard deviations in the data from sample groups CA2, CA3 and CC1 (see Table 3). However in regions of low energy input, the cricket populations consist almost entirely of the microphthalmic type, producing low standard deviations in the data from sample groups CA1, CC2 and CC3. The assumption that significant differences exist in the composition of the cricket populations of energy-rich and energy-poor regions within the same cave is supported by the results of the Mann-Whitney U test.

TABLE 3

The relationship between the number of corneal lenses of crickets and the level of energy input into their habitat.

Sample group number	Level of energy input	Mean of corneal lens counts	Standard deviation
CA3	very high	149.93	54.90
CA2	high	127.90	58.39
CA1	low	72.90	14.14
CC1	high	94.25	34.42
CC2	low	74.83	16.84
CC3	very low	61.00	7.42

In general, the estimated level of energy input is directly related to the mean c.l.c. and standard deviation in the sample group from each collection area: the lower the energy input, the lower the mean and standard deviation. This correlation suggests that the microphthalmic type of crickets can survive with much less food than the macrophthalmic type, a feature presumably adaptive to a troglobitic existence. It is therefore possible that the two types of crickets represent a troglobitic subspecies and its troglophile ancestor, either in the process of parapatric speciation, or which evolved allopatrically and have recently come into contact, resulting in some miscegenation.

The wide range of eye sizes and degrees of pigmentation of the 'macrophthalmic type' suggests that inheritance of both of these characters is polygenic. Alternatively, the variability in eye size and pigmentation may represent a wide norm of reaction, rather than a high degree of heterozygosity, in which case crickets from 'deep cave' populations may have reduced eyes and pigment because of some environmental effect or lack of a necessary stimulus (absence of light or of a dietary factor) during development to maturity. This does not contradict the possibility of two subspecies being represented in the caves, but would tend to blurr the phenotypic distinctions between them. Obviously, genetic and rearing studies are needed to resolve these various alternatives.

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APPENDIX

Raw data — Numbers of corneal lenses per eye (corneal lens count)

Cueva el Coy Coy de Uria

Group 1 CC1		Group 2 CC2		Group 3 CC3	
No.	determination	No.	determination	No.	determination
61	em	51	em	52	1m
63	em	59	em	60	em
66	em	63	em	62	em
67	em	65	em	70	1m
118	1m	66	em		
120	1m	67	em		
126	1m	73	em		
133	1m	74	em		
		81	1m		
		95	1m		
		101	1m		
		103	1m		

Cueva de Camburales

Group 1 CA1		Group 2 CA2		Group 3 CA2	
No.	determination	No.	determination	No.	determination
53	em	60	em	63	em
57	1m	62	em	64	em
58	1m	64	em	66	em
59	1m	66	em	71	em
60	em	66	em	151	1m
60	1m	68	em	162	1m
63	1m	125	1m	162	1m
63	1m	130	1m	169	1m
63	1m	135	1m	176	1m
65	em	140	1m	177	1m
67	em	145	1m	185	1m
69	em	156	1m	187	1m
70	1m	195	1m	198	1m
73	1m	203	1m	206	1m
73	1m	210	1m	212	1m
74	1m	221	1m		
75	1m				
75	1m				
76	1m				
77	1m				
80	1m				
81	1m				
83	1m				
84	1m				
85	1m				
87	1m				
101	1m				
120	1m				

photographed through:
em = scanning electron microscope
1m = light microscope (binocular)