

which are shown in the illustration. Two of the six pupae (remember one larva drowned) were likewise preserved whole, and four adult *cupressi* moths emerged under indoor conditions in early October. The pupal cases of these latter were unearthed from the sand in the cages, and were all found at approximately the same depth and in the same type of cells as mentioned above.

The pupa is dark brown, about 3.5 cm in length and on the moderately slender side. It lacks a free tongue case. Its surface is punctate on all sides, though ventrally the abdominal segments are smooth posteriorly. It should be noted in passing that while our pupae agree in description with that given by Bates (1928) except for the placement of the punctae, none of our reared larvae reached the length quoted by that authority of 65 mm, though the four emerging adults were of normal size.

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## BEHAVIORAL ADAPTATIONS OF CRYPTIC MOTHS. VI. FURTHER EXPERIMENTAL STUDIES ON BARK-LIKE SPECIES

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Prior studies have demonstrated that a number of bark-like moths will select appropriate backgrounds in various experimental apparatuses which provide a choice of backgrounds differing in reflectance (Kettlewell, 1955; Sargent, 1966; Sargent & Keiper, 1969). Several experiments indicate that these selections are based on innate preferences of the moths for certain background reflectances (Sargent, 1968, 1969a, b).

The present paper summarizes additional experiments which shed light on (1) some factors promoting "errors" in the background selections of

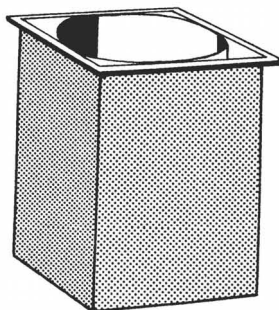


Fig. 1. The experimental apparatus used in the present studies.

moths in experimental situations, and (2) the nature of the background selection process itself. The experiments were carried out during the summers of 1970 and 1971 in Leverett, Franklin County, Massachusetts.

#### General Methods and Materials

The basic apparatus in all of the experiments consisted of a cylinder (19 in. high  $\times$  44 in. circumference) made up of blotting paper sections, set into a plywood box (19 in. high  $\times$  15 in. square), and covered with a pane of window glass (Fig. 1). The blotting paper sections were painted black, gray, or white, and so provided a choice of backgrounds differing in reflectance. (The percentage-reflectance values of the backgrounds, as measured with a General Electric recording spectrophotometer against a white standard of pressed  $\text{BaSO}_4$ , were: black 4.30, gray 39.50, and white 85.61.) The apparatus was placed in a wooded area, and moths were introduced into the cylinder at night by sliding the glass top to one side. Background selections of the moths were noted shortly after dawn on the following morning.

#### The Experiments and Results

EXPERIMENT 1. Early observations suggested that some species which are known to select appropriate backgrounds in nature (e.g. *Catocala relictata* Walker (Noctuidae) which prefers to rest on white birch trees; Keiper, 1968; Sargent & Keiper, 1969) did not exhibit background preferences in the present experimental apparatus. It was noted, however, that the background selections of these moths might vary according to their position in the apparatus, as moths resting at the very top of the cylinder, i.e. immediately adjacent to the pane of glass, were very often over an inappropriate background. Therefore an experiment was conducted, using reared *Catocala relictata* (Sargent, 1972), in which the precise posi-

TABLE 1. Experiment 1: Background selections of *Catocala relictata*.

Position within Cylinder	Number of Moths		P*
	White Background	Black Background	
At Top	7	8	> 0.90
Below Top	10	0	< 0.01

\* Based on chi-square tests of goodness-of-fit to a 1:1 distribution.

tions of the moths, as well as the background selections, were recorded. The experimental cylinder for this experiment consisted of alternating black and white sections (each  $11 \times 19$  in.).

The results of this experiment (Table 1) clearly revealed that moths resting at the top of the cylinder did not exhibit a background preference, while moths resting at lower levels preferred the white backgrounds. It would appear that some behavior, perhaps a phototactic or geotactic escape response, interfered with the background selections of certain moths in this experimental situation.

EXPERIMENT 2. Another factor which seemed to influence background selections in the experimental apparatus was the number of moths tested on any given night. Accordingly, a simple experiment was conducted with *Phigalia titea* (Cramer) (Geometridae), a species known to prefer pale backgrounds (Sargent, 1969b). In this experiment, tests of background selections were carried out using samples of from 1–30 individuals in the experimental apparatus. The moths were collected at lights, and the experimental cylinder in this case consisted of a white, gray, and black section (each  $14.7 \times 19$  in.).

The results of this experiment (Table 2) showed that there was a critical sample size of about 20 individuals, below which a background preference was clearly exhibited, and above which no background preference was shown. This finding suggests that some behavioral interaction,

TABLE 2. Experiment 2: Background selections of *Phigalia titea*.

Sample Size	No. Tests	Number of Moths			P*
		White Background	Gray Background	Black Background	
1–10	9	18	7	8	< 0.05
11–20	3	21	10	7	< 0.02
21–30	2	19	19	15	> 0.70

\* Based on chi-square tests of goodness-of-fit to a 1:1:1 distribution.

TABLE 3. Experiment 3: Background selections of *Cosymbia pendulinaria*.

Experimental Condition	Number of Moths		P*
	White Background	Black Background	
Without Acetate Cylinder	55	6	< 0.001
With Acetate Cylinder	30	2	< 0.001

\* Based on chi-square tests of goodness-of-fit to a 1:1 distribution.

presumably one resulting from the mutual intolerance of individuals and functioning to disperse the moths, interfered with background selections at high densities in this experimental apparatus.

EXPERIMENT 3. Some question has been raised about the ability of bark-like moths to select appropriate backgrounds from a distance, i.e. when not in direct physical contact with a substrate (e.g. Kettlewell, 1955; Ford, 1964). If contact were required, then it might be argued that thermal, rather than visual, cues were playing the important role in background selections. In that event, moths would be detecting and responding to small, surface temperature differences associated with backgrounds of different reflectances.

In order to test this possibility, the experimental apparatus was equipped with a cylinder of clear cellulose acetate which could be set within the cylinder of blotting paper sections, and which separated experimental moths from the painted backgrounds by approximately two inches. The species tested was *Cosymbia pendulinaria* Gueneé (Geometridae), which prefers white backgrounds (Sargent, 1968). The painted cylinder in this experiment consisted of alternating black and white sections (each 11 × 19 in.), and moths were tested for background preferences when the acetate cylinder was absent (controls) and present (experimentals). It was assumed that the separation of moths and backgrounds by the acetate cylinder was sufficient to prevent detection of any surface temperature differences.

The results of this experiment (Table 3) showed that direct physical contact with the backgrounds was not required for the moths to exhibit a background reflectance preference.

#### DISCUSSION

The results of Experiments 1 and 2 indicate that considerable care must be taken in the design and execution of experiments which are intended as tests of background preferences in cryptic moths. Certain behaviors, particularly escape and avoidance responses, may be elicited

in some individuals and under some circumstances in an experimental apparatus, and these behaviors may interfere with background preferences. Thus, a failure to detect background preferences may result from inadequacies in an experimental test, rather than from inability of the moths themselves.

The results of Experiment 3 tend to corroborate the prevailing view that background reflectance preferences of bark-like moths are based on responses to visual stimuli. This conclusion is strengthened by field observations of released individuals of *Cosymbia pendulinaria* (and *Catocala relictata*; Sargent & Keiper, 1969). In these field tests, the erratic escape flight of certain individuals would become directed after some seconds, and this directed flight (sometimes up to 50 feet in length) usually led to an appropriate background (white birch tree). This observation, the results of Experiment 3, and numerous other experimental results (Sargent, 1968, 1969a, b) fail to support the reflectance-matching mechanism proposed by Kettlewell (1955) and Ford (1964) to explain the selection of appropriate backgrounds by bark-like moths. On the contrary, all of the evidence to date supports the view that these background selections are genetically fixed, or innate, responses.

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