Journal of The Lepidopterists' Society

Volume 23 | 1969 | Number 1

BEHAVIORAL ADAPTATIONS OF CRYPTIC MOTHS. I. PRELIMINARY STUDIES ON BARK-LIKE SPECIES

Theodore D. Sargent and Ronald R. Keiper
Department of Zoology, University of Massachusetts, Amherst

Bark-like cryptic resemblance, as a defensive adaptation of moths, has both static and dynamic components. The colors and patterns of moths are fixed during development, and this static element necessitates dynamic elements, if cryptic resemblance is to succeed as a deceptive stratagem in predator-prey relationships. The dynamic elements are of two types: 1. selection of appropriate backgrounds, in terms of reflectance, hue, and pattern; and 2. adoption of appropriate resting attitudes, which maximize the moth-background resemblances. Figures 1 and 2 illustrate the results of appropriate and inappropriate choices of background and resting attitude in two cryptic species. [For other examples, consult the reviews of Poulton (1890) and Cott (1940).]

Our interests, over the past two summers, have centered on these dynamic, or behavioral, elements involved in the cryptic adaptations of bark-like moths. Both field observations and experimental studies have been carried out, and this paper presents some early results of this work. All of the studies reported here were conducted in Franklin and Hampshire counties in central Massachusetts, during the summers of 1966 and 1967.

Field Observations

Two techniques were employed in our studies on the normal resting habits of cryptic moths. The first of these simply involved searching tree trunks for resting moths. When found, a moth was photographed, and extensive notes regarding the moth and its resting place were taken. These notes included references to the species of tree selected, the resting height of the moth, and its resting attitude.

The second technique involved releasing color-marked moths in wooded areas and following them to their resting places. These moths were captured at lights or "sugar," kept overnight in experimental boxes, and released the following morning. A spot of Flo-Paque paint was applied to

Figure 1. The noctuid, *Catocala relicta* Walker, at rest on an appropriate (upper) and inappropriate (lower) background on paper-birch, *Betula papyrifera* Marsh. Drawing by K. A. Doktor-Sargent.

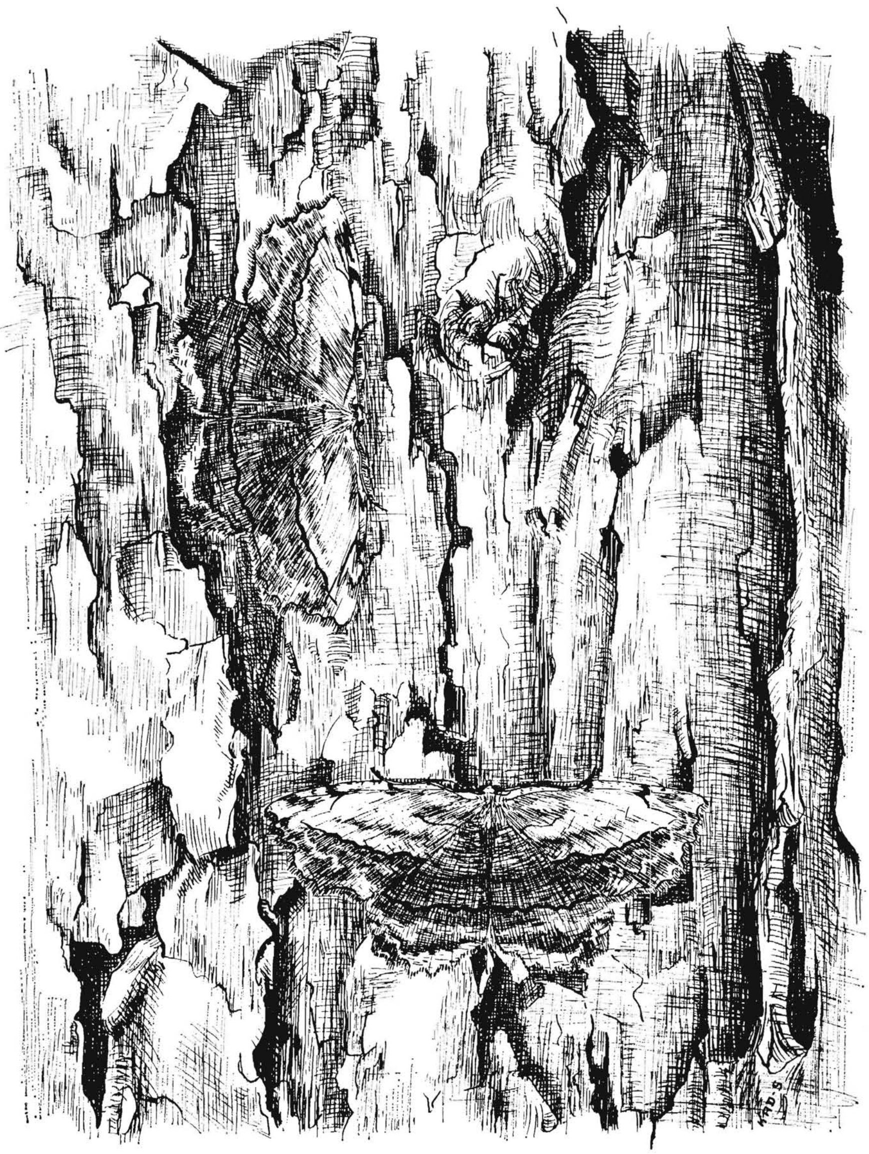

Figure 2. The geometrid, *Lytrosis unitaria* Herrich-Schaeffer, at rest in an appropriate (upper) and inappropriate (lower) resting attitude on red oak, *Quercus rubra* L. Drawing by K. A. Doktor-Sargent.

one forewing of each moth, making later identification in the field possible. Here, as with the undisturbed moths, photographs and notes were taken.

The two techniques yielded very similar results for any given species. The resting attitudes of undisturbed and released individuals were almost invariably identical. The species of trees selected and the resting heights, while more variable, were often remarkably similar in undisturbed and released individuals.

A good example of these similarities is provided by our results with *Catocala relicta* Walker (Noctuidae). We found six undisturbed individuals of this species, and released five others. All of these moths rested with the head up, and eight (four in each group) selected paper-birch (*Betula papyrifera* Marsh) for a resting substrate. The average resting height of the undisturbed moths was 8 feet (range 4–12 feet), and of the released moths was 10 feet (range 7–15 feet).

Table I summarizes our observations on 25 of the most common species encountered on tree trunks. These field observations suggested that some cryptic moths are able to select appropriate backgrounds, and further, instinctively orient themselves on these backgrounds so as to heighten their cryptic resemblance. In order to test these possibilities, a number of experiments were carried out. Three of these experiments will now be described.

TABLE I. FIELD OBSERVATIONS OF COMMON BARK-HAUNTING SPECIES.

Species (Numbers: Undisturbed, Released)	Usual Resting Attitude	Comments
GEOMETRIDAE		
Semiothisa ocellinata Guenée (120+, 0)	sideways	pale trees, e.g., gray birch, red maple; usually within 2 ft. of ground
Melanolophia canadaria Guenée (25, 0)	sideways	often conifers; average height 6 ft.
Lytrosis unitaria Herrich-Schaeffer (3, 3)	sideways	from 3–5 ft.
Cosymbia pendulinaria Guenée (200+, 10)	head up	pale trees, primarily gray and paper birch; average height 5 ft.
Xanthorhoë intermediata Guenée (13, 0)	head down	variety of trees; usually less than 4 ft. from ground
Lobophora nivigerata Walker (6, 0)	head up	gray birch; from 3–8 ft.

TABLE I. CONTINUED

Species (Numbers: Undisturbed, Released)	Usual Resting Attitude	Comments
NOCTUIDAE		
Mamestra adjuncta Boisduval (6, 0)	head up	variety of trees; average height 4 ft.
Apatela innotata Guenée (4, 0)	head up	paper birch; from 5–10 ft.
Catocala antinympha Hübner (3, 8)	head down	often dark trees; average height 5 ft.
Catocala vidua Smith & Abbot (14, 10)	head down	many tree species; average height 5 ft., but often very low
Catocala ilia Cramer (2, 16)	head down	many tree species; average height 17 ft., often very high
Catocala relicta Walker (6, 5)	head up	prefers paper birch; average height 9 ft.
Catocala unijuga Walker (2, 3)	head up	variety of trees; average height 14 ft.
Catocala cara Guenée (1, 6)	head down	often sugar maple; also under eaves; average height 9 ft.
Catocala concumbens Walker (5, 7)	head down	prefers smooth-barked trees; also on fence-posts; average height 4 ft.
Catocala gracilis Edwards (9, 12)	head down	variety of trees; often in furrows; average height 6 ft.
Catocala andromedae Guenée (4, 4)	head down	similar to *C. gracilis*
Catocala ultronia Hübner (7, 31)	head down	variety of trees; often white pine, near whorl of branches; average height 8 ft.
Catocala crataegi Saunders (0, 20)	head down	often large white pine; average height 9 ft.
Catocala grynea Cramer (1, 4)	head down	average height 6 ft.
Catocala praeclara Grote & Robinson (1, 4)	head down	average height 5 ft.
Catocala micronympha Guenée (2, 7)	head down	often on oaks; average height 6 ft.
Catocala amica Hübner (15, 5)	head down	often on oaks; average height 7 ft.
Epizeuxis aemula Hübner (20+, 0)	head down	many tree species; from 3–6 ft.
Epizeuxis americalis Guenée (50+, 0)	head down	many tree species; from 5–7 ft.

EXPERIMENTAL STUDIES

Our experiments have been designed primarily to assess the importance of background reflectance and hue in the selection of substrates by cryptic moths. One experiment was designed to shed some light on the stimuli which dictate the moths' resting attitudes.

The basic piece of apparatus in these experiments consisted of a plywood box (15 inches square by 19 inches high), into which a cylinder (44 inches in circumference and 19 inches high) was set. This cylinder was made up of blotting paper sections which were painted, or otherwise treated, to provide a selection of backgrounds for the moths. The apparatus was covered with a pane of window glass and a double layer of cheesecloth, and was placed in a wooded area where a thick canopy excluded direct sunlight. Moths were introduced into the cylinder by sliding the glass top to one side.

The moths were collected at lights or "sugar," and immediately released into the experimental boxes. The following morning, between 0600 and 0800 EST, the background selections of the moths were noted.

REFLECTANCE

The field observations suggested that bark-like moths might select trees of appropriate reflectance—light moths preferring light trees such as gray birch, *Betula populifolia* Marsh, or red maple, *Acer rubrum* L.; and dark moths preferring dark trees such as white pine, *Pinus strobus* L., or red oak, *Quercus rubra* L. Accordingly, a number of species were tested for background preferences in an experimental apparatus allowing a choice between black and white backgrounds. (Basically this apparatus consisted of two white and two black 11 × 19 inch pieces of blotting paper, formed into a cylinder of alternating black and white sections.)

Some of the results of this experiment are summarized in Table II, and these illustrate the general finding that bark-like cryptic moths tend to select backgrounds which match the reflectance of their forewings. Similar results have been reported previously (Kettlewell, 1955; Sargent, 1966), and an experiment with painted moths (Sargent, 1968) suggests that these background selections are genetically fixed, and are not based on an ability of the moths to compare themselves with their backgrounds.

HUE

Since most bark-haunting moths are relatively achromatic, an experiment was designed to determine whether such moths would avoid backgrounds of appropriate reflectance, but inappropriate hue. The experimental apparatus was similar to that used previously, but here eight backgrounds were presented—six achromatic grays, one yellow, and one green.[1]

Results obtained with the geometrid, *Cosymbia pendulinaria* Guenée, are presented in Figure 3. Obviously individuals of this species preferred the palest gray backgrounds, and generally avoided the equally pale chromatic backgrounds (there were significantly fewer moths on the yellow and green backgrounds than on the two palest gray backgrounds; chi-square 25, P less than 0.001).

Although this result might be due to a relative insensitivity of the moths to the yellow and green hues presented, existing data on color vision in insects (*e.g.*, Goldsmith, 1961) would not support such an interpretation. It appears that these avoidances of the moths were based on hue characteristics of the yellow and green backgrounds. A stronger conclusion, however, must await further advances in our understanding of insect color vision.

Resting Attitude

Since field observations indicated that most bark-like moths adopt species-specific resting attitudes on tree trunks, an experiment was devised in an attempt to determine the factors responsible for this behavior. The experimental apparatus was similar to those used previously, but here

[1] Hue and reflectance characteristics of the backgrounds and moths were obtained with a General Electric recording spectrophotometer. Details of the techniques employed may be found in Sargent (1966). The X, Y, Z coordinates for the yellow and green backgrounds were respectively 72.03, 77.00, 29.80; 49.48, 57.15, 62.76.

Table II. Selection of Backgrounds by Light and Dark Species in an Experimental Apparatus.

Family[1]	Species	Backgrounds		P[2]
		Black	White	
LIGHT MOTHS				
G	*Semiothisa ocellinata* Guenée	2	10	*
G	*Eufidonia notataria* Walker	5	15	*
G	*Cosymbia pendulinaria* Guenée	2	19	***
N	*Apatela innotata* Guenée	1	9	*
DARK MOTHS				
N	*Mamestra adjuncta* Boisduval	9	1	*
N	*Mamestra detracta* Walker	12	2	**
N	*Chytonix palliatricula* Guenée	14	3	**
N	*Catocala antinympha* Hübner	23	1	***

[1] Families: G = Geometridae; N = Noctuidae.
[2] Significant deviations from chance selections of the black and white backgrounds (chi-square tests) are indicated by asterisks for probabilities (P) of less than 0.05 (one *), 0.01 (two **), and 0.001 (three ***).

the backgrounds were varied by means of black tape strips applied to pieces of white blotting paper. In this manner, four backgrounds were made up—two with vertical strips, and two with horizontal strips. (These strips were either one-sixteenth or one-eighth inch wide, and were spaced at one-half inch intervals. The difference in tape widths was not significant in the present experiment.)

In addition, a second cylinder of clear acetate was constructed which could be set within the cylinder made up of the taped backgrounds. When in place, this acetate cylinder shielded the moths from any tactile stimuli associated with the tape strips, but allowed visual stimuli to pass.

The results of an experiment using a noctuid which invariably rests with its head down, *Catocala gracilis* Edwards, are shown in Figure 4. All 32 individuals tested in this experiment, with or without the acetate cylinder in place, rested with the head down. However, a significant preference for the vertical strips was shown only when the acetate cylinder was not in place. These results suggest that the basic stimulus dictating a moth's resting attitude is rather general (*e.g.*, gravity), and is not related to the immediate surroundings. On the other hand, it seems apparent that tactile stimuli, which are directly related to the

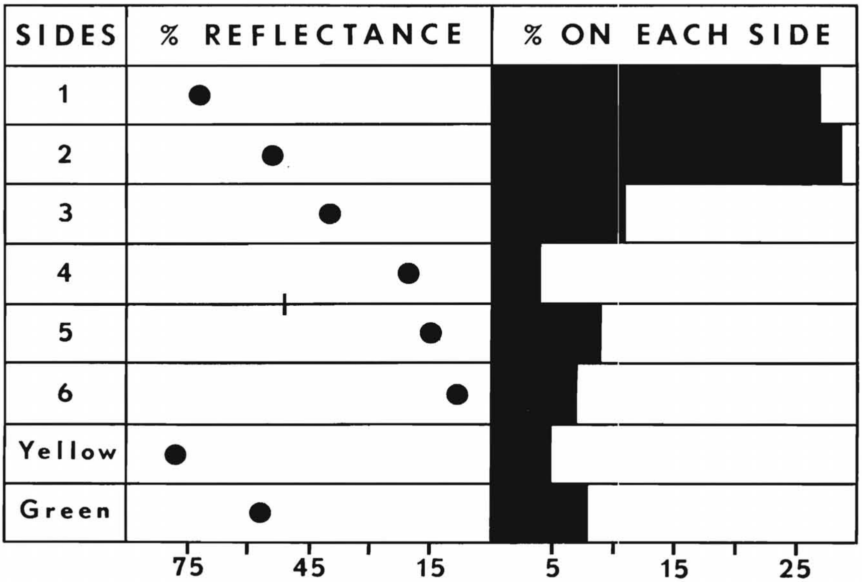

Figure 3. Reflectances of backgrounds in an eight-sided experimental apparatus, and the percent of 92 *Cosymbia pendulinaria* selecting each of these backgrounds. The reflectance of the moths' forewings is indicated by the short vertical line within the figure.

CONDITIONS	BACKGROUNDS & NOS. OF MOTHS Vertical	Horizontal	P
Without Acetate Shield	12	1	★★
With Acetate Shield	7	12	ns

Figure 4. Background selections of *Catocala gracilis* in an experimental apparatus consisting of backgrounds with vertical and horizontal tape strips. Results are shown for two conditions—with and without an acetate shield in front of the taped backgrounds. The significant deviation from a chance distribution on the two backgrounds is indicated by two stars for a probability (P) of less than 0.01; ns = not significant.

immediate substrate, may be important in the selection of a final resting place.

Summary

Behavioral adaptations of bark-like cryptic moths were studied in central Massachusetts during the summers of 1966 and 1967. Both field observations and experiments were carried out.

The release of marked moths in the field seemed to provide reliable information about normal resting habits, as results obtained using this method compared favorably with those obtained from undisturbed moths.

The experiments involved the use of an apparatus, basically consisting of a cylinder made up of blotting paper sections which were painted, or otherwise treated, to provide a selection of backgrounds. Results of these experiments indicated that reflectance, hue, and tactile properties of backgrounds are factors which influence the resting choices of cryptic moths.

Acknowledgments

Financial support for these studies was provided by a Faculty Research Grant from the University of Massachusetts.

We would like to thank Dr. F. J. Francis of the Department of Food Science and Technology, University of Massachusetts, for his assistance in the determination of moth and background reflectances.

Literature Cited

Cott, H. B., 1940. Adaptive Coloration in Animals. Methuen, London. xxxii + 508 pp.

Goldsmith, T. H., 1961. The color vision of insects. *In:* W. D. McElroy & B. Glass, eds., Light and Life. Johns Hopkins Press, Baltimore. pp. 771–794.

Kettlewell, H. B. D., 1955. Recognition of appropriate backgrounds by the pale and black phases of lepidoptera. Nature, 175: 943.

Poulton, E. B., 1890. The Colours of Animals. Appleton, New York. xiii + 360 pp.

Sargent, T. D., 1966. Background selections of geometrid and noctuid moths. Science, 154: 1674–1675.

1968. Cryptic moths: effects on background selections of painting the circum-ocular scales. Science, 159: 100–101.