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FREQUENCIES OF THE MELANIC MORPH OF *BISTON COGNATARIA* (GEOMETRIDAE) IN A LOW-POLLUTION AREA OF PENNSYLVANIA FROM 1971 TO 1978

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ABSTRACT. The frequency of melanics in *Biston cognataria* was monitored for eight years in a low-pollution area near Klingerstown, Pennsylvania. A total of 3148 specimens was taken by UV light trap, on 528 nights; fewer than 1% were females. Over the long period a fairly stable equilibrium was maintained at about 52% melanics. There were only two statistically significant year-to-year deviations in melanic frequency—a rise in 1973 and a decline in 1978. No clear directional shift was evident. There was no significant difference in frequencies between the first and second annual generations. Fluctuations in abundance and in several climatic factors during this study period did not affect the melanic frequency.

Industrial melanism in many species of cryptic moths has been widely studied in Great Britain and some areas of the European continent (summarized by Kettlewell, 1961, 1973; Robinson, 1971). In North America the documentation is not yet extensive, but evidence of long-term increases and possibly decreases in frequency of melanic moths appears to be emerging (Kettlewell, 1957, 1958, 1961; Remington, 1958; Owen, 1961, 1962; Sargent, 1969, 1974), often in close relatives of the European species.

Kettlewell (1973) estimated that over 100 species in North America may prove to show melanic polymorphism. Owen (1962) listed 20 species of American Geometridae showing significant melanism, based on his rapid examination of museum collections. Sargent (1974) reported on six of these species he had followed in Massachusetts over a five-year period. In my current studies in central-eastern Pennsylvania, beginning in 1971, the nightly operation of a light trap for sampling *Biston cognataria* (Guenée) has also revealed abundant melanics of *Phigalia titea* (Cramer), *Ectropis crepuscularia* (Denis

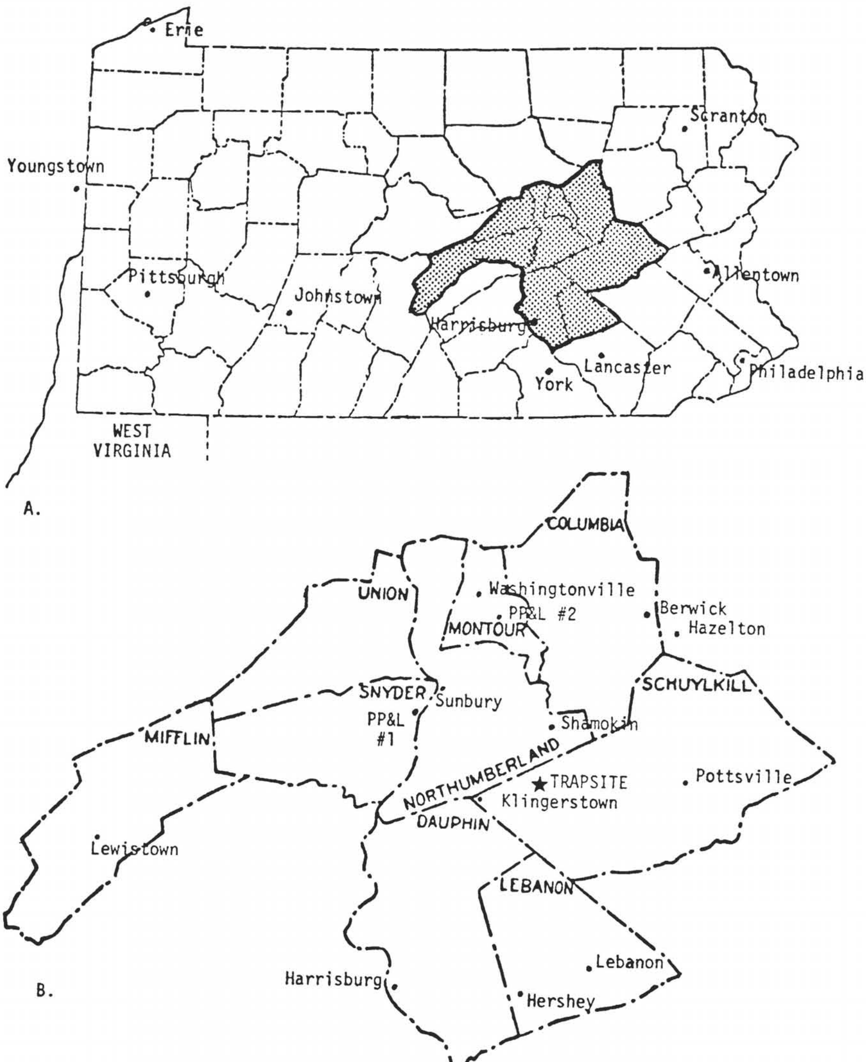

FIG. 1. (**A**) County map of Pennsylvania showing the location of the major industrial cities. Those west of the stippled area are potential sources of gaseous pollution critical to corticolous lichens and *Lycia* at the trapsite. (**B**) Counties surrounding the trapsite, with principal industrial areas capable of producing gaseous pollutants designated.

& Schiffermüller), *Epimecis hortaria* (Fabricius) and *Charadra deridens* (Guenée), and an occasional melanic of *Catocala ultronia* (Hübner).

The change in the flora of eastern North America, beginning with the decline of the last major glaciation around 12,000 years b.p., with coniferous forests being extensively replaced by broad-leaved trees and high rainfall and humidity, probably provided excellent conditions for lichens to cover tree trunks. Lichens, however, are extremely sensitive to the gaseous pollution that results from industrialization in North America as in Europe (see, e.g., Kettlewell, 1973). Thus a reduction in the pale corticolous lichens, or their elimination in extremely polluted areas, plus blackening of tree trunks by soot accumulation, probably provided a new cryptic background for melanic phenes of bark-resting moths. Sargent (1974) suggested that another human activity, logging, selectively removed mature trees, such as white pine with lighter furrowed bark, causing a new prevalence of younger trees with darker smooth bark; this also would favor melanics. He further suggested that long before European colonization and industrialization, forest fires may have repeatedly blackened vast areas, making dark resting moths the most cryptic. All of these conditions favor melanic forms of corticolous Lepidoptera.

Biston cognataria is one of the most abundant geometrids exhibiting melanism in central-eastern Pennsylvania. Increases in the melanic form of this moth have been noted by many lepidopterists in the vicinity of highly industrialized areas (see, e.g., Owen, 1961, 1962; West, 1977).

Although the Palearctic *Biston* (*Biston* acvt) *betularia* L. may have been separated from *B. cognataria* for many thousands of years, hybrids between these species are at least partially fertile (Kettlewell, 1955, 1959; West, 1977), and they are morphologically very close and may prove to be the same biological species (see, e.g., Rindge, 1975). It is thus not surprising that melanism in *B. cognataria* appears to parallel that of *B. betularia* (e.g., Robinson, 1971; Kettlewell, 1973).

This paper reports eight years of recording the incidence of the melanic phene ("swettaria") of *B. cognataria* and the non-melanic phene in a relatively pollution-free environment. New potential sources of pollution are being built in the area, especially coal-burning power plants and an experimental coal gasification plant in Shamokin, and I intend to continue the sampling for several years to monitor melanic frequencies for comparisons with the pre-industrial period reported here.

SAMPLE SITE AND METHODS

The sampling area (see map, Fig. 1B) is an isolated tree-covered mountain and valley environment with small, cleared areas of pasture and field corn, 12 km northeast of Klingerstown, Schuylkill Co., Pennsylvania. This sampling area is 30 km southeast of Sunbury, Pennsylvania, location of a large coal-burning power plant; it is 55 air km north-northeast of Harrisburg and 37 air km west of Pottsville, the other nearest areas of major pollution. The nearest small city, Shamokin, 17 km to the northeast and at present not a major source of pollution, is separated by the heavily forested Mahanoy Mountains. Since the wind movement is primarily west to east, the nearest windward major polluter is Lewistown, 83 air km west. Several mountain ranges and the broad Juniata and Susquehanna river valleys probably influence air movement and cause significant reduction of pollutants prior to arrival of Lewistown air at the collecting area.

Among pollutants, it is interesting to note that the level of acid precipitation in Pennsylvania is one of the highest in the eastern United States (Likens et al., 1979), but the acid rain and snow have not eliminated the corticolous lichens that are usually considered the pivotal factor in tree-trunk color to which resting *Biston* are adapting (see, e.g., Kettlewell, 1973).

A tripod light trap with funnel opening about 1 m above the ground, with a 15-watt blacklite fluorescent tube as the ultraviolet source and with a cyanogas killing chamber, was operated nightly from 1 May to 15 September each year. The trap was emptied each day and all specimens of *Biston cognataria* and other potential industrial melanic species were saved, pinned, and later spread for study.

Daily recordings of minimum and maximum temperatures were made at the trap site. These, plus precipitation, cloud cover, fog and phases of moon are the subject of a separate paper on annual and seasonal abundance of *B. cognataria,* along with snow cover and depth, freezing periods and above-ground temperatures for the winters preceding each sample set.

Voltinism

The present study did establish that *Biston cognataria* in Pennsylvania is bivoltine, as two distinct generations were obvious when the sample numbers were large. The first generation normally emerges during the later part of May, peaks during mid-June, with a rapid decline by the second week of July. The second generation commonly emerges in late July, peaks during the third week of August, and rapidly declines during the first week of September. This conclusion is further supported by the lack of pupal diapause in the brood produced by a female taken 12 May 1973. All pupae of this latter brood hatched by mid-August of that year. Since the melanic frequency did not change between the early and late generations each year (see below), seasonal physical factors will not be examined closely in the present paper.

The Tree-Trunk Substrate

The normal resting place for *Biston* is on the trunks of trees, where, as expected for a palatable cryptic moth, they indeed blend with the background. As a tree-trunk rester, it is potentially vulnerable to visual predation by birds; thus, strong selection must exist for site selection behavior favoring crypsis (Tingergen, 1960; Kettlewell, 1973).

Although natural resting sites of *Biston cognataria* have not been extensively recorded, Kettlewell (1973, p. 108) stated for *B. betularia* in England that "both sexes spend the day at rest on the boughs and trunks of trees," and the same seems likely for *B. cognataria* in North America.

It is, therefore, of importance to note the tree types of the research area. The tree community near the trap consists of the following predominant species. Eight have pale trunks, *Quercus alba* L., *Acer rubrum* L., *A. pennsylvanicum* L., *Betula populifolia* Marsh., *Fraxinus lanceolata* Sarg., *Robinia pseudoacacia* L., *Juglans cinerea* L., and *Populus grandidentata* Michx. The common dark-barked species are *Quercus rubra* L., *Juglans nigra* L., *Cornus florida* L., *Pinus strobus* L., *P. virginiana* Mell., *Tsuga canadensis* L., *Prunus serotina* Ehrh., *Acer saccharinum* L., and *Tilia americana* L. Two intermediate-colored species, *Carya ovata* Koch and *Liriodendron tulipifera* L., provide a fairly suitable background color for both forms of the moth, depending on the part of the tree used for resting. Trunks are often lichen-covered at least on the northern side. With the rather uniform distribution over the area of different tree species presenting a range of black colors, suitable resting sites were readily accessible to both forms and moths could be so evenly dispersed that predator searches are minimally productive.

Melanic Frequency

A wide range of melanic frequencies of *Biston cognataria* have been reported in North America. In Livingston Co., Michigan, a highly industrialized area, samples from 1951 to 1961 were 87.0 to 93.0% melanic (Owen, 1961). In Leverett, Massachusetts, a non-industrialized area, samples for 1971 to 1974 ranged from 0 to 5.6% melanic (Sargent, 1974, 1976). These represent the recorded extremes for *Biston* melanism in North America.

Table 1 shows the distribution of melanic frequencies in the population samples taken in the present study in east-central Pennsylvania. During the eight-year study covering 1059 potential trapping nights, a total of 3148 *Biston* were taken on 528 nights. Less than 1% are females, perhaps due to the elevated position of the trap opening. The moths were grouped into 190 four-day samples for analysis. Data

TABLE 1. The numbers and percentages of melanic forms of *Biston cognataria* in each generation and for the season trapped near Klingerstown, Pennsylvania (1971–1978).

Year	Generation	Number melanic	Number non-melanic each brood	Percent of melanic each brood	Percent of melanics for season
1971	1	140	134	51.1	
	2	167	147	53.1	52.2
1972	1	126	114	52.5	
	2	214	215	49.9	50.8
1973	1	247	182	57.6	
	2	216	183	54.2	55.9
1974	1	51	55	48.1	
	2	91	75	54.8	52.2
1975	1	2	1	66.0	
	2	51	48	51.5	52.0
1976	1	40	32	55.5	
	2	76	71	51.7	52.9
1977	1	59	51	53.6	
	2	65	69	48.5	50.8
1978	1	22	35	38.6	
	2	82	87	48.5	46.1
Totals	1	687	604	53.2	
	2	962	895	51.8	
		1649	1499	52.4	

acquired from this site are more comprehensive than from sites previously reported and have been subjected to a wider range of tests.

In separating my melanic from non-melanic forms the breeding experiments with *B. betularia* by Clarke & Sheppard (1964) and Kettlewell (1963) were used as guidelines; those authors showed that incomplete dominance exists for melanics of that species. Modifiers quantitatively dilute the black pigment, creating a descending scale of phenotypic forms between the jet black ("carbonaria"), dark gray (most "insularia"), and the lightest ("typica"). Owen (1962) recognized similar forms in *B. cognataria* in North America and suggested the operation of a similar gene complex. However, more recently Clarke (1979) has noted the difficulty in distinguishing phenotypically the two dark forms "insularia" and "carbonaria" in *B. betularia.* Faced with the same assay problem with my trapped *cognataria,* I scored as "melanic" only the very darkest phenotypes. For guidance I was aided by a brood reared from a wild Pennsylvania female, all known to be homozygous for the recessive, non-melanic allele. These show the usual slight variations in the suffusion of black scales, not related to the incompletely dominant allele for the full melanic, and helped me to score as "non-melanic" the moderately dark forms taken at the trap. Some of these dark individuals appear nearly black; however, the typical pattern of the non-melanic was visible beneath the heavy suffusion of black scales covering the wings and body of the moth. To establish a degree of uniformity in scoring the trap samples, only those moths whose color exceeded that of the darkest individuals in the reared brood were considered to be true melanics and were included in the melanic count. The number of the dark intermediate forms difficult to classify taken in the trap represented only 6.2% of the "melanic" population (some were present in both annual generations). Since the difficult individuals were so few, and the criteria were used equally for all years' samples, any errors in the phenotypic assay could not have influenced the results significantly.

From an examination of Table 1, two major questions can be answered: First—"Are there changes in melanic frequency from year to year?"; second—"Is there a shift in the frequency of melanics from the early, diapausing, generation to the summer non-diapausing generation?"; note that the early generation emerging from pupal diapause would have been subject to low winter and spring soil temperatures surrounding the pupae, and the summer generation would have developed under a more uniform and higher pupal temperature range, with moisture being the principal variant.

As the statistical analysis summarized below showed, there was no significant shift in frequency from the first to second generation each season. There were four years where the melanic frequency increased from 2.17%–9.93% in the second generation, over the first; three years the melanic frequency decreased by 2.61%–6.31% in the second generation. The small shifts do not appear to be environmental responses in Darwinian selection, as the largest difference during 1978 showed a rise in melanic frequency in the second generation of 9.93, following the most severe winter of the study and average summer temperatures, while the second largest rise, 6.69 in 1974 followed the mildest winter and an average summer; nor did the smallest negative shifts in the second generation follow any pattern of climatic variation.

For analysis within each generation, some four-nightly samples were pooled so that samples with 15 or more moths were obtained throughout, with most containing 25 or more. The significance of year-to-year and first-to-second generation variation in melanic frequencies was then examined via a two-way analysis of variance (ANOVA), on arcsine transformed data, using the methods of Sokal & Rohlf (1969; with correction for unequal subclass numbers, Steel & Torrie, 1960).

Table 2 shows the ANOVA results over the entire span of years,

TABLE 2. Analysis of changes in melanic frequency by generations and years. Two-way ANOVA on arcsine transformed data as discussed in text. Year-year variation in melanic frequencies is highly significant, while generation-generation variation and year-generation interactions are not.

Source	df	SS	Ms	F	
A (years)	7	558.62	79.80	3.82	$P < .001$
B (generations)	1	6.49	6.49	.31	$.75 > P > .50$
A × B	7	199.74	28.53	1.37	$.25 > P > .10$
Within	75	1565.98	20.88		
Total	90	2349.74			

and for both generations per year. Highly significant variation among years is seen, but not between the two yearly generations. Yet Table 1 suggests that even the yearly frequencies are similar if the two most deviant from the 8-year mean (1973, 1978) are excluded. In order to test homogeneity of various yearly sets, several further tests were performed.

First, the most deviant frequencies relative to the 8-year mean were excluded—one by one—and the remaining sets analyzed for significant year to year variation in melanic frequency, again using ANOVA. The 1978 sample (lowest frequency) was omitted, and year-to-year variation was still found to be significant ($F_{6,68} = 2.61$, $.025 > P > .01$). Exclusion of the 1973 sample (highest frequency) also indicated significant remaining year-to-year variation ($F_{6,58} = 2.29$, $.05 > P > .025$). After omission of both 1973 and 1978, however, the year-to-year variance component fell far below significance ($F_{5,51} = 1.02$, $.50 > P > .25$). Both year-generation and generation-generation (early vs. late) interactions remained insignificant throughout ($.25 > P > .10$, or greater). Using a **second**, fundamentally similar approach, transforms of melanic frequencies were pooled among generations within years and these yearly samples searched for significance by a sum of squares simultaneous test procedure (SS-STP; see Gabriel, 1964). Here again, exclusion of both 1973 and 1978 produced a set of samples without significant differences (SS = 78.8, $.50 > P > .25$). Excluding only 1973 makes the remaining set just marginally homogeneous (SS = 237.5; $.10 > P > .05$), while excluding only 1978 shows higher heterogeneity (SS = 338.0, $P < .05$). A Student-Newman-Keuls analysis also returns similar sets of significantly different samples (.05 level). These latter two analyses (SS-STP, SNK) complement the ANOVA in showing that the years 1971, 1972, 1974, 1975, 1976, 1977 exhibit a homogeneous array of melanic frequencies, with 1973 and 1978 representing significant divergent frequencies.

These data show a fairly stable equilibrium between melanics and non-melanics, with occasional perturbations above and below the mean. No clear directional trend in melanic frequency is yet apparent when all eight years are examined together (Spearman rank correlation; $R = 0.43$, $p > .20$ two-tailed). After 1973, however, the yearly means suggest a gradual decrease in melanic frequency ($R = 0.83$, $p = .086$ two-tailed). The 1979, 1980 and 1981 sequels to the 1978 decrease will be of special interest. Continued sampling of *Biston cognataria* at this locality is underway and projected.

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