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THE ENVIRONMENTAL REGULATION OF SEASONAL DIMORPHISM IN *PIERIS NAPI OLERACEA* (PIERIDAE)

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The causes of seasonal changes in the coloration, wing marking pattern, and even wing and body structure of Lepidoptera have long been an intriguing subject for experimentation. The changes may be of two basic types: either a marked but continuous shift in intensity and extent of pattern elements or ground color, or a sharply defined dimorphism in which colors and pattern elements may be completely replaced and changes in wing and body structure may occur. The former type is common in continuously brooded species such as *Colias eurytheme* Boisduval and *Phyciodes tharos* Drury, while the latter occurs most often in discretely brooded species such as *Araschnia levana* L. and *Celastrina argiolus* L.

Two chief factors, temperature and photoperiod, have so far been shown to be of importance in regulating seasonal forms. In *Precis octavia* Cramer the effect is caused entirely by rearing temperature (McLeod, 1968). The appearance of female *Ascia monuste* L., which may vary in color from white to dark gray (Pease, 1962) and the seasonal dimorphism of *Pieris protodice* Boisduval & LeConte (Shapiro, 1968) are, on the other hand, due to daily photoperiod exposure during the immature stages. The forms of other species such as *Araschnia levana* (Süffert, 1924; Müller, 1955, 1956) and *Colias eurytheme* (Ae, 1957) apparently are regulated by a synergism between temperature and photoperiod.

Pieris napi oleracea Harris is sharply bivoltine in eastern North America. The spring and summer broods differ markedly in body to wing size proportions and in the extent and intensity of wing pattern (Table 1). The experiments described here were designed as an attempt to produce the seasonal forms shown in nature using temperature and photoperiod as controlled variables.

TABLE 1. Differences in appearance between "spring" and "summer" phenotypes of *Pieris napi oleracea*.

"Spring" phenotype	"Summer" phenotype
1. Body relatively stout, dark, hairy.	Body relatively slender, lighter-colored, smooth.
2. Dorsal dark scaling at wing bases and forewing apex heavy.	Dorsal dark scaling light.
3. Scaling along veins on underside of hind wing always very dark, complete, clear-cut.	Scaling along veins on underside of hind wing varying from light and complete, to light and incomplete, to absent.

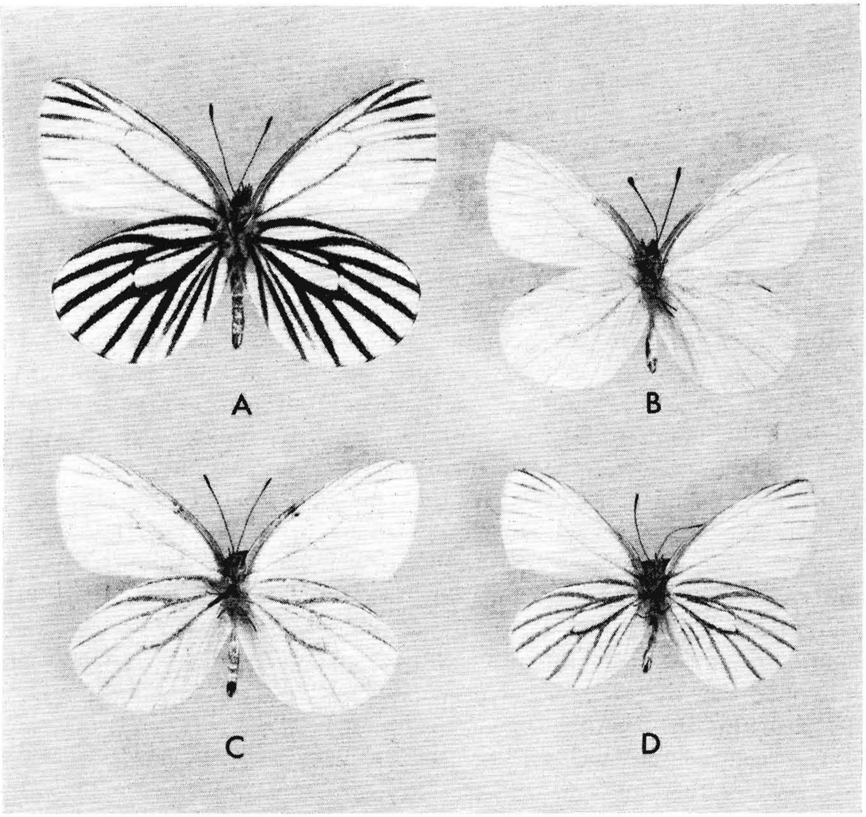
Procedure

Four broods of *P. n. oleracea* were derived from wild-inseminated females collected 15 May 1968 at Wahconah Falls State Park, Berkshire Co., Massachusetts. The newly hatched larvae of three of the females were divided into two lots for rearing both on long days, short nights (15hL/9hD) and on short days, long nights (12hL/12hD), while those of the fourth female were reared only on long days, short nights. All of the larvae were fed on cut mustard leaves (*Brassica*) and given a 25° C day and a 22° C night.

None of the pupae produced from long-day larvae entered diapause, and are hereafter referred to as the non-diapausing pupae. Among these emergence or death occurred in every case within six to ten days. None of the pupae produced from short-day larvae had emerged after two to three weeks and were thus presumed to have entered diapause (the diapausing pupae). They were placed at 5° C in darkness for 10 weeks to terminate diapause.

Immediately after pupation the non-diapausing pupae were subdivided into four lots and redistributed to await adult development under the following temperature and photoperiod regimes: 25° C day, 22° C night, 15hL/9hD (N = 14); 25° C day, 22° C night, 12hL/12hD (N = 13); 25° C day, 15° C night, 16hL/8hD (N = 12); 25° C day, 5° C night, 16hL/8hD (N = 18). Mortality of the pupae was 8/65 (12.3%), due probably in some cases to cold shock.

The diapausing pupae were left on their larval temperature and photoperiod regimes until the onset of chilling. After removal from cold, they were subdivided into three lots, all kept on long days and at 25° C during the day, but with night temperatures of 22° C (N = 14), 15° C (N = 8), 5° C (N = 8). Hatching of 30/43 (69.8%) of the pupae occurred six to 18 days after removal from cold. The death of another pupa occurred before 18 days after chilling, while the other 12 pupae were kept at



Figs. A–D, *Pieris napi oleracea*, ventral view of males. A, "Spring" adult from diapausing pupa; B–D, extreme light, medium, and extreme dark "summer" adults from non-diapausing pupae. (All laboratory-reared progeny of wild-caught females from Berkshire Co., Mass., 15 May 1968.)

room temperature for several months and gradually desiccated without ever hatching.

Results

The results were unequivocal. In each case the non-diapausing pupae produced adults typical of the "summer" phenotype, while the diapausing pupae produced typical "spring" adults. There was no correlation of phenotype to any environmental factor except larval photoperiod exposure. Each of the four broods gave the same range of adult variation in coloration as found in the wild summer emergence (Table 1 and Figs. C and D). The diapausing pupae gave adults all almost identical in appearance to each other, regardless of pupal photoperiod and temperature regime (Figs. A and B).

Discussion

Clearly the basic environmental factor determining seasonal form in *P. napi oleracea* is larval photoperiod exposure. However, it is impossible as yet to say whether it is larval photoperiod itself or the occurrence of diapause in the pupa that actually directly determines which phenotype is to be produced, since larval photoperiod and diapause cannot here be separated.

It is interesting that even though part of the non-diapausing pupae were chilled overnight during the time when adult wing pigment was being formed, there was no darkening effect at all shown in the emerging adults. This seems to be in contradiction to Merrifield's (1893) report that chilling summer pupae of British *P. napi* L. caused the emerging adults to have "most, but not all, of the characteristics of the spring form." Merrifield's pupae were, however, chilled for three to four months prior to exposure to spring (average 54° F) or summer (average 80° F) conditions during development. There was no further intensification of dark markings in the lot exposed to spring conditions. Probably the pupae had entered diapause at the onset of the three or four months of chilling, but it may be that *P. n. napi* has a rather different system for the regulation of seasonal forms from that of *P. n. oleracea*.

The results indicate that *P. n. oleracea* in eastern North America has two systems that regulate the appearance of the adult phenotype. The first is the inherited, environment-independent expression of dark wing markings in the "summer" form. This system is responsible for the individual variation found in the summer brood. The second is the environmentally induced "switching on" of the "spring" form. Since this involves uniformly maximum expression of the characters that show variation in the summer form, as well as new differences, any genetic variation in wing pattern that would be revealed in the summer brood is concealed in the spring brood.

Summary

Diapausing and non-diapausing pupae of *Pieris napi oleracea* were exposed to various photoperiod and temperature regimes during adult development. The pupae which had undergone diapause produced only adults of the "spring" form, whereas those that had not, produced only adults of the "summer" form. Regulation of seasonal dimorphism is thus

controlled by larval photoperiod exposure, which also controls the induction of pupal diapause.

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