PHOTOPERIODIC REGULATION OF SEASONAL POLYPHENISM IN *PHYCIODES THAROS* (NYMPHALIDAE)

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The useful but not widely known term "polyphenism" was introduced by Mayr (1963) and refers to any sort of intrapopulation phenotypic variation that is not directly genetic. It thus includes all environmentally regulated variation that is shown in the phenotype. Seasonal polyphenism in Lepidoptera is regulated by environmental factors, and, as I have discussed in a previous paper (Oliver, 1970), may be manifested either as a discontinuous shift in phenotypic appearance or as a continuous shift in the range of phenotypic variation along a gradient. In either case the environment triggers an initial genetic response in the organism which canalizes development toward a "seasonal form."

Seasonal polyphenism in multivoltine populations of *Phyciodes tharos* Drury belongs to the discontinuous type. The wings of summer adults (form "morpheus" Fabricius, Figs. 1, 2) tend to be less intensely colored than those of spring and fall adults (form "marcia" Edwards, Figs. 3, 4). This tendency is more pronounced on the ventral sides of the wings and is most extreme in late winter individuals from the southern part of the range (e.g., Cedar Key, Florida). Table 1 gives a comparison of the phenotypic appearances of the two forms. A great range in color variation is shown in any sample at any location at any time of year. The adaptive significance of a basically similar phenomenon in *Colias* (Pieridae) has been discussed by Watt (1968).

The chief factors responsible for the regulation of seasonal polyphenism in Lepidoptera are photoperiod (Pease, 1962; Shapiro, 1968) or temperature (McLeod, 1968) alone or a synergism between the two (Ae, 1957). Klots (1951) implies that it is exposure to cold in the pupal stage that induces the "marcia" form, but no experimental evidence is presented. The experiments described here were designed to test the response of *P. tharos* to different photoperiod and temperature regimes during the larval and pupal stages.

PROCEDURE AND MATERIALS

Laboratory breeding stock was derived from three wild-inseminated females. One female was collected 4 mi. E Cedar Key, Levy Co., Florida,

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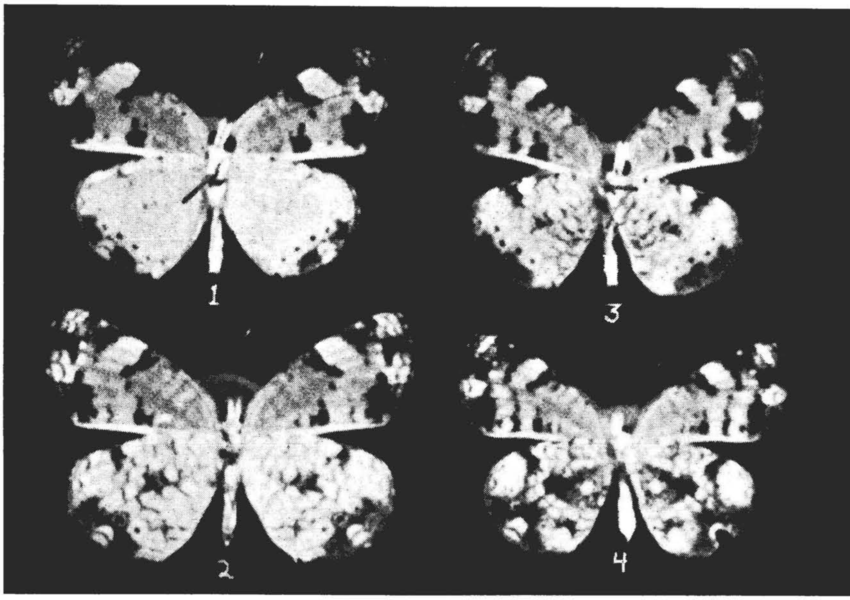
TABLE 1. Comparison of phenotypic appearance of most contrasting specimens of seasonal forms "marcia" and "morpheus" of *Phyciodes tharos*.

"marcia"	"morpheus"
Dorsal	
1. Submarginal spots clear, contrastingly pale.	Spots obsolescent, dark gray if present.
2. Marginal and submarginal black lines light and separated.	Black lines fused into a band.
3. Male forewing postmedian black markings well expressed.	Dark markings obsolescent, making an open light area.
Ventral (Hindwing)	
Males	
1. Brown markings heavy, smudgy.	Brown markings thin, crisp.
2. Silver crescent spot bright, blurry.	Crescent covered by submarginal dark patch.
Females	
1. Brown markings heavy, very smudgy, filling areas between light spot bands.	Markings forming a thin, crisp brown reticulation.
2. Basal, median, submarginal light bands suffused with silver-white.	Crescent spot only silver-white present, light bands straw yellow.

29 March 1969, and the others 4 mi. N Emporia, Sussex Co., Virginia, 3 May 1969. Populations from these areas appear similar in phenotypic appearance and are indistinguishable in the laboratory. Potted *Aster ericoides* L. served as the oviposition site and larval foodplant. The newly-hatched larvae in each brood were divided into a long day, short night group (15hL, 9hD) and a short day, long night group (10hL, 14hD). Both groups were given a 25°C day and a 22°C night. When the short day group entered the third instar, it was divided into two lots, one of which was kept on the same temperature regime, and the other of which was given a 25°C day and a 5°C night. These regimes were maintained through the pupal stage and until adult emergence. Cultures were maintained in climate-controlled growth chambers with a temperature fluctuation of less than 2°C during each temperature period. Artificial lighting was provided with fluorescent tubes of the "sunlight" type. Chilling to 5°C was carried out in an unlighted domestic refrigerator.

RESULTS

The adults from the long day, short night group (N = 21) were of the "morpheus" form (Figs. 1, 2), whereas those from the short day, long night group (N = 46) were all of the "marcia" form (Figs. 3, 4).



Figs. 1–4. *Phyciodes tharos*: 1 & 2, form "morpheus" reared on photoperiod regime of 15hL, 9hD; 3 & 4, "marcia" reared on 10hL, 14hD.

No phenotypic differences were observed in the responses of the two population samples. Differences in temperature regime in the short day group had no apparent effect on adult phenotype. These laboratory-reared broods of *P. tharos* showed great phenotypic homogeneity compared to wild-collected samples.

Discussion

Seasonal polyphenism in *Phyciodes tharos* is controlled by photoperiod. The fall and spring "marcia" form is induced by the comparatively short days and long nights of late summer and early spring. Fall "marcia" have apparently developed without larval diapause, whereas spring "marcia" have undergone diapause. "Morpheus" is due to the long days and short nights of early and mid summer.

Phenotypic variation in wild seasonal samples of *P. tharos* may be attributable to differences in larval photoperiod exposure as well as to individual genetic variation. The intensification of the "marcia" appearance in southern U.S.A. samples (where the growing season ends and begins with shorter days and longer nights than in the northern U.S.A.) indicates that the effect is a graded one in nature.

There was no incidence of diapause among the *P. tharos* larvae on either photoperiod regime. Regulation of diapause in this species has not been investigated, but it may be influenced by larval temperature exposure during the first two instars. In any case diapause and polyphenism seem to have no direct link in this species.

SUMMARY

Photoperiod regulates expression of the seasonal forms of *Phyciodes tharos*. A larval and pupal photoperiod regime similar to that of early summer produced adults all of the "morpheus" form, whereas a regime similar to that of late summer produced only "marcia." Larval and pupal temperature exposure had no effect on adult phenotype.

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