TABLE 25

The photoperiodic reaction (percentage of winter females) of geographical populations of the mite *Metatetranychus ulmi* (after Geispits, 1960)

Population	Day-length in hours					
	13	14	15	16	17	24
Leningrad (60° N.)	100	100	100	100	94·1	0
Southern England (50° N.)	94·0	54·0	4·0	0	—	0
North China (40° N.)	16·6	6·2	0	0	0	0

variations in climate. These are expressed in the formation of local races possessing different norms of reaction to photoperiodic conditions. As one moves to the north—i.e. with increase in latitude—one observes a regular increase in the threshold of day-length. In the above cases both the general direction of variation and even the amounts of variation of critical day-length are similar.

The connection between the physiological characteristics of local races and their phenology and life cycles in different zones will be discussed below, but the general ecological significance of these adaptations is already fully evident. A higher light threshold for photoperiodic reaction leads to earlier calendar dates for onset of diapause in northern zones, in spite of the longer days there.

Our attention is drawn to the remarkable analogy between inherited variations in photoperiodic reaction with adaptation to geographical conditions, and variations in this reaction caused by the temperature conditions during the developmental period. As has been shown, a fall in temperature during the developmental period produces a marked and regular increase in critical day-length, and may even completely suppress the photoperiodic effect, causing monocyclism to appear. Geographically speaking, temperature usually falls with increase in latitude. Consequently, inherited or phenotypical adaptations will in natural conditions operate in the same direction. This creates an ecologically-unified mechanism, synchronizing the life cycle with the changes of climatic conditions.

In the examples of *Acronycta rumicis* and *Barathra brassicae* it can be seen that the geographical populations studied, with

their evident differences in average critical thresholds, actually form a continuous series, and that the extreme individual divergences of adjacent forms are close or even overlap. In other words, here we have a typical case of clinal variation in the reaction that regulates diapause, corresponding to a gradual latitudinal change in day-length. Therefore there are no grounds for seeking clearly-defined geographical ranges for the separate local races of these species. Such clinal variation, however, is not

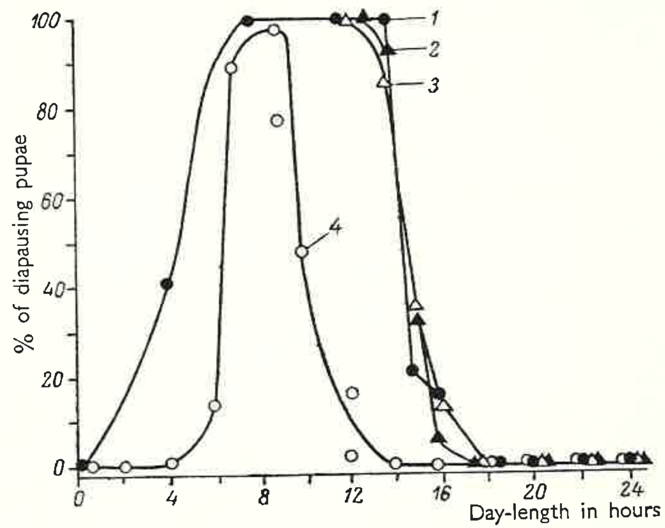

FIG. 32. The geographical variation in the photoperiodic reaction in *Pieris brassicae*. Temperature 23°.

Populations: 1, Leningrad (60°N.); 2, Brest (52°N.); 3, Belgorod (50°N.); 4, Abkhazian (43°N.).

found in all species. Even among those studied by us we have observed cases where a large part of the range was occupied by a monotypic race. A typical example is the Cabbage White Butterfly *Pieris brassicae*, whose photoperiodic reaction is illustrated in Fig. 32. In experimental investigations of stocks obtained from Leningrad, Brest, and Belgorod provinces, a completely identical type of photoperiodic reaction was observed in all populations, with a critical day-length of 15 hours. (The same critical day-length has also been discovered in a Northern Caucasus (Essentuki) population of *Pieris brassicae*.)

Phenological data show that the greater part of the European territory of the USSR is occupied by precisely this form of the Cabbage White Butterfly. Analysis of the phenology of this species in Central Asia and Transcaucasia, however, gives grounds for believing that in the extreme south of its range there exists another form, which requires a considerably shorter day for induction of diapause. This is confirmed by study of the Abkhazian population, which, as is seen from Fig. 32, is markedly

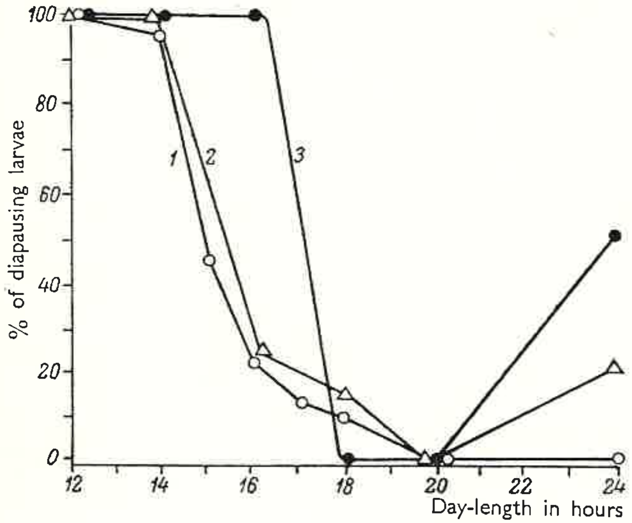

FIG. 33. The geographical variation in the photoperiodic reaction in *Pyrausta nubilalis*. Temperature 25° (from data of Du Chzhen'-ven').

Populations: 1, Abkhazian (43°N.); 2, Dnepropetrovsk (48°N.); 3, Sumy (52°N.).

different from the more northern forms. At a temperature of 23° the northern form reacts definitely to change in day-length, and with photoperiods from 14 to 8 hours of light all pupae enter diapause. In the Abkhazian form the photoperiodic effect appears within very narrow limits at these temperatures. Complete diapause is observed only with day-length of about 9 hours, and the critical threshold appears with a 10-hour day.

Another example of gradual variation in photoperiodic reaction is provided by the European Corn Borer *Pyrausta*

nubilalis, investigated by Du Chzhen'-ven' (Fig. 33). In experiments at a temperature of 25°, southern populations from Abkhazia and the steppe zone of the Ukraine (Dnepropetrovsk) showed similar values for critical day-length of approximately 15 hours of light per day, in spite of the considerable distance between them (6° of latitude). A population from northern Ukraine (Sumy province), although geographically closer to that from Dnepropetrovsk, differed greatly from it in having a higher threshold value (17 hours) and a much higher percentage of diapausing pupae when developing in continuous 24-hour light.

Thus we may say that in *Pyrausta nubilalis* there are two geographical races, differing in photoperiodic reaction, with the boundary between them lying along the south of the forest-steppe zone. Apparently these races correspond to the forms mentioned in the literature—the 'hemp' form, which in nature is univoltine, and the 'maize' form, which produces (partly or wholly) two generations.

Similar relationships appear in the butterfly *Hylophila prasinana* L. This species is of interest because in it geographical variation in reaction to day-length is combined with marked dimorphism of the adults. In Chapter I it was shown that the Sukhumi race of this species, in short-day conditions, produces diapausing pupae, from which the 'typical' *Hylophila prasinana* emerge in spring. With long days its development does not include diapause and a differently-coloured summer form emeges, which was formerly thought to be the independent species *H. hongarica* Warr. Extension of the southern dimorphic race to the north has gone as far as the Ukraine forest-steppe zone (Poltava). But from Belgorod province northwards to Leningrad one finds only the monocyclic race of the *Hylophila prasinana* L. type. Even in long-day conditions it is not possible to obtain non-diapause development and the summer form in this race.

Differences in the nature of intraspecific physiological differentiation, observed in various species, lead to the conclusion that the gradient in geographical variation in photoperiodic reaction is determined not only by external conditions (gradual variation in day-length with latitude) but also by the biological peculiarities of a species.

In order to evaluate the significance of photoperiodic conditions as a factor inducing formation of intraspecific local races, we quote also the results of observations on other species of polycyclic Lepidoptera, as yet less fully studied.

Wide variations in critical thresholds of photoperiodic reaction have been observed in the pierids *Pieris rapae* and *P. napi* (Fig. 34) and the arctiid *Spilosoma menthastri* (see Fig. 48). Comparison of the development of Leningrad and Belgorod populations of several species of polycyclic Lepidoptera in short-day and long-day conditions shows that there are always distinct inherited

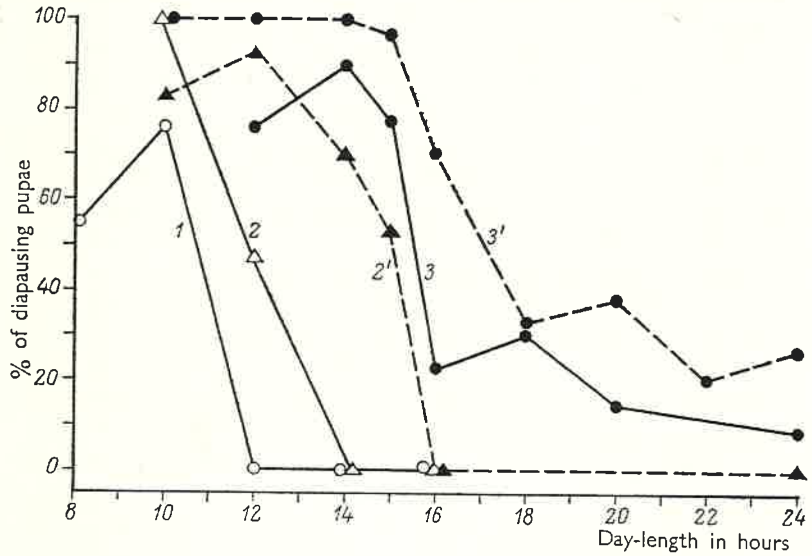

FIG. 34. The geographical variation in the photoperiodic reaction in *Pieris rapae* and *Pieris napi*. Temperature 23°.

Populations: 1, Sukhumi; 2 and 2′, Belgorod; 3 and 3′, Leningrad.
—— *Pieris rapae*; – – – *Pieris napi*.

differences between them. The Belgorod populations of *Smerinthus populi*, *Acronycta leporina*, *A. megacephala*, *Demas coryli*, *Pandemis ribeana*, and *Capua reticulana*, at a temperature of 21°-23° and in long-day conditions (18 hours), develop without diapause, whereas in similar conditions the majority of individuals in the northern populations enter diapause (DANILEVSKII, 1957a). Short days induce diapause in both southern and northern forms.

The formation of local races as a result of geographical

variation in day-length is observed not only in free-living phytophagous species but also in blood-sucking mosquitoes.

The decisive role of day-length in regulation of the gonotrophic cycle and diapause in the malaria mosquito *Anopheles maculipennis messeae* and the common mosquito *Culex pipiens pipiens* has been demonstrated experimentally by DANILEVSKII and GLINYANAYA (1958) and VINOGRADOVA (1958). SHIPITSYNA (1959), on the basis of personal field observations and analysis of extensive phenological data for the whole of the USSR, confirmed that imaginal diapause in the malaria mosquito depends on light conditions during the period of development of the aquatic stages. In this connection she drew attention to the fact that in different climatic zones diapause commences when day-length has different values. The critical day-length always, however, differs from the maximum for the locality by a more or less constant amount—$1\frac{1}{2}$ to 2 hours. Shipitsyna expressed the opinion that the onset of diapause in the malaria mosquito is affected not by the absolute duration of daylight but by its decrease by a definite number of hours. From this suggestion it follows that the norm of reaction to the light conditions has a constant value for a species.

New experimental investigations by Vinogradova (1960), however, did not confirm Shipitsyna's hypothesis. Comparison of populations of *Anopheles maculipennis messeae* from Leningrad and Astrakhan showed that adaptation to light and temperature conditions in different latitudes leads to the formation of intraspecific local races differing in their particular requirements. As with other species, the southern forms of mosquitoes are characterized by considerably lower threshold values than those of the northern forms. Thus in the malaria mosquito we must differentiate not only the long-known subspecies but also local races within these subspecies, with inherited differences in features of their life cycles.

In the field of geographical variation the seasonal cycles of parasitic insects are of great interest. The conformity of the life cycles of parasitic insects and of their hosts has been explained by the direct dependence of the parasite's development on changes in the physiological condition of the host (SALT, 1941). From this point of view it seemed unreasonable to expect special adaptations to geographical conditions in parasites. But GEISPITS and KYAO (1953) showed by experiment that in the endoparasitic ichneumon