IS THE DIAPAUSE IN INSECTS ERADICABLE?

By E. P. Wiltshire, F.R.E.S.

Cousin's experimental study on the diapause in insects is the chief work on this subject. It deals principally with Diptera. Experiments by others on Lepidoptera are also quoted in it, and Cousin reconciles these with the conclusions he forms from his own experiments. He is doubtless right in regarding the diapause as a phenomenon equally developed and equally capable of study in different Orders of Insects.

Cousin's experiments showed that the diapause, as observed by him —whether hibernation or aestivation—is the consequence of unfavourable external conditions rather than heredity; and he concluded that a diapause can be eliminated by rearing several generations in optimum conditions, each species having its own optimum, to which, he states, natural conditions rarely if ever approximate. He expressly warns us against judging a species by its natural behaviour.

There are innumerable Lepidoptera, with a long strong diapause in a state of nature which might be cited as warranting objection to Cousin's conclusions, but his warning against argument from natural behaviour (a warning which is perhaps not admissible) requires us to experiment with breeding these species over several generations and trying to find their optimum conditions. The warning, in effect, obliges any prospective opponent to his views to contest them with weapons of Cousin's own choosing; it imposes inevitably a considerable delay on the prospective opponent, if it does not actually prevent him altogether from venturing on to the field. Meanwhile, until the necessary protracted experiments can be made and published, the fallacy in Cousin's conclusions needs pointing out, to prevent the other side's case going by default.

The fallacy lies in the fact that Cousin *selected* his subjects. He selected them for their suitability for experimental breeding. For this purpose the most suitable subjects are continuously-brooded species with a short life cycle; and Cousin's selections are indeed all continuously-brooded species (e.g., *Lucilia sericata*, Meig., *Calliphora erythrocephala*, Meig., *Phormia groenlandica*, Zett., and *Mormoniella vitripennis*, Walk.). Cousin uses the term " poly-voltine " for this type of phenology; to a purist, " multi-voltine " would be a preferable word.

Yet the multi-voltine or continuously-brooded species are those in which the diapause is weakest; small wonder that a study of the diapause in these insects should lead the author to conclude that it is a reaction to external circumstances rather than a fixed inherited factor. The longest diapause he succeeded in producing in *L. sericata*, his main subject, was of less than a month. The extreme cases in nature, however (to omit mention of cases of " overlying " for more than a year), have a diapause lasting nine or ten months (e.g., *Simyra dentinosa*, Stgr., *Cucullia strigicosta*, Bours., *Cucullia faucicola*, Wilts., *Epitherina rhodopoleos*, Wehrli, *Itame berytaria*, Stgr., etc.). These extreme cases, and the cases of pupal rest prolonged over a year or more, are of " univoltine " or single-brooded species. A study of the diapause in insects should surely concentrate on univoltine species. Jarvis' study, therefore, though less thorough-going, is superior to that of Cousin because it distinguishes better between species with different phenologies, and also, of course, because of its bio-chemical approach.

I have found that the diapause is strongest in species restricted to the more arid parts of the world, i.e. the Southern Palaearctic or Sub-Tropical rather than the Northern-Palaearctic or Euro-Siberian, and presumably also in the Tropical (i.e. regions within the Tropics with a distinct dry season) rather than the Equatorial (i.e. regions close to the Equator with a more distributed rainfall) climatic regions. The extreme cases are mostly desert or steppe species. In these areas a strong diapause (aestivation) occurs in many insects with more than one annual generation, but is longest and most obstinate in the single-brooded (univoltine), i.e. I have found that the diapause in some bi-voltine (two-brooded) species is broken down to some extent by breeding conditions differing from the natural. The phenomenon of hibernation, on the other hand, which is so marked in the Euro-Siberian Zone, and may occur twice or even more often in one life-cycle in Sub-Arctic climates, may be of a different bio-chemical character from the diapause produced by heat and aridity.

The very fact that the species with the strong diapause are restricted to regions with a generally unfavourable climate points to the probability that their diapause is inherited and uneradicable, otherwise we would expect to find them also inhabiting the more favourable climates. Alternative possible reasons for their limited range are foodplant-specialization (extreme monophagy) or one of those mysterious biological conditions to which we refer when we say that a species is past its climax or no longer has the impulse to extend its range. Without going here into cases and details, I consider both these alternatives less likely as explanations of the restricted range of these species than a rigid life-cycle (i.e. *inter alia* an obstinate diapause) combined with stenoecism (no tendency to migrate) and a lack of ecological tolerance.

The following Lepidoptera are quoted by Cousin:—*Carpocapsa pomonella*, L., *Lasiocampa quercus*, L., *Dendrolimus pini*, and *Pyrausta nubilalis*. For these he quotes the conclusions reached by Pictet and Babcock. Pictet states that after six generations bred at 22° C., *quercus* loses its diapause entirely; *pini* is said to react similarly. Whether this experiment proved lethal to any number of larvae is not stated. *Quercus* is the only univoltine species mentioned in the whole of Cousin's article with any details of experimental results. Yet it is not a good example for studying the diapause, for its hibernation seems to be a mere retardation by cold, and not a true diapause such as Jarvis designated as " true hibernation " (Jarvis found that " true hibernators " when hibernating did not react to heat by resuming their vital process). The choice of a uni-voltine species with a more rapid rate of growth than *pini* or *quercus* and a " true hibernation " might have produced different results from those reported by Pictet. Babcock's results with *nubilalis*, as given by Cousin, are of considerable interest. This species, of considerable economic importance, seems to be what in previous articles on phenology I have classified as " partly two-brooded." I gave as a type of this class *Notodonta ziczac*, L. Babcock found that " under normal conditions " 14% *nubilalis* larvae were univoltine, and that under hot dry conditions this proportion increased to 72%. This showed that heat and aridity strengthened the diapause, but that the diapause was still " normal " under more favourable conditions.

Cousin's experiments themselves cannot be contested; the general conclusions he draws from them are probably valid for all insects with

phenologies similar to those on which he experiments; the experiments reveal the probable way in which the diapause has evolved from the most primitive multivoltine phenologies, parallel with the evolution of the biological alternative, migration; but the general conclusions cannot, in my view, be applied generally to all insects, and especially not to those in which the diapause has developed most strongly. Indeed, I also doubt whether a marked diapause can be artificially produced in multivoltine species which have evolved, as an alternative, the migratory tendency in response to unfavourable environments. In fact, I consider Cousin's conclusions more applicable to the evolving species, those whose phenologies are still rather fluid, than to the fully-evolved species.

In all my ten years of breeding Lepidoptera in the Middle East, only once did a single-brooded species with a long diapause emerge out of season; that was when a pupa of *Cucullia lychnitis*, Ramb., produced an adult one month after pupation instead of waiting till the following Spring. Individual exceptions like this admittedly occur, but are not evidence that *lychnitis* would, if experimented on, cease to be univoltine.

I believe that the question could be settled in Britain without recourse to experiments on the extreme cases, which, being Sub-Tropical, are difficult for British entomologists to obtain. I appeal therefore to British breeders of Lepidoptera to make experiments on *Anthocharis cardamines*, *Thera rupicapraria*, *Cheimatobia brumata*, *Amathes lychnidis*, *Brachionycha sphinx*, and other species with similar phenologies. I believe that it will prove impossible to eradicate the diapause of these species in the way Cousin thought possible. I should also like to see confirmation of Pictet's experiments with *quercus*. And if any breeder has already made observations relevant to this discussion, I hope he will report them at once without waiting to make elaborate and protracted experiments.

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IRISH LEPIDOPTERA COLLECTING IN 1944.

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1944 was a bad year for Lepidoptera in Ireland. There was a deplorable scarcity of even the commonest species, and this was particularly noticeable amongst the Geometers. For example, ten hours' collecting in a good locality in Abbeyleix on 22nd July produced only six species. However, the marsh Lepidoptera were at least as numerous as usual, some species, for example *Aphantopus hyperantus*, being exceptionally common. Nevertheless, the season's collecting produced at least two species new to the Irish list and 119 new county records. The latter figure is not as impressive as it sounds, as the majority of these records are from Co. Leix, from which virtually no previous records