Modes of Protection in the Pupal Stage of Butterflies and Moths.

BY

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The chrysalis stage of butterflies and moths is exposed to special dangers. The perfect insects themselves can escape by flight and are very quick to detect the approach of an enemy. At night and in cloudy weather the diurnal species remain hidden among thick leaves or in hollow recesses in trees or banks. The larvae can conceal themselves by day and come out to feed at night, and when detected can escape by falling to the ground among the dense herbage. But the chrysalis is comparatively helpless, and with very rare exceptions, can do nothing to defend itself or escape when once it is discovered. Hence we find that such a large proportion of moth chrysalises bury in the ground and possess a colour which renders them inconspicuous if exposed by an enemy digging or turning over the dead leaves. Many species, however, especially those with a short pupal period, do not bury, but are either enclosed in cocoons—the method adopted by many moths and the "skippers"—or are freely exposed, as in butterflies generally and occasionally in moths. In both these methods special adaptations are employed as a protection against enemies. It must always be borne in mind that insect-eating animals are as a rule sharp-sighted and observant, that the wonderful results produced are the outcome of a race between the keen senses of enemies and the protective devices of insects, and that, when what appears to be the climax of perfection is reached, the race still goes on and keeps up the high standard.

A good example of the sharpness of enemies is well shown by an observation made in 1900 by Mr. A. H. Hamm in his garden in Oxford. The cocoons of the Lackey moth (*Malacosoma neustria*, L.) are woven of silk rendered opaque and probably rather unpleasant in the mouth by an abundant yellow powder made up of crystalline carbonate of lime in the form of aragonite. This is secreted by the renal (Malpighian) tubules, but retained in them until the cocoon is made, when it is extruded by the caterpillar and rubbed into the silken walls. These yellow cocoons, formed upon leaves of the foodplant, are thick on the exposed side but thin where they are woven against the leaf, and the sparrows in Mr. Hamm's garden had found this out and extracted the chrysalises by pecking a hole through the leaf and the thin part of the cocoon (*Proc. Ent. Soc. Lond.*, 1902, p. xv.).

The most perfect concealment also often fails before the tactics of enemies. Nothing could be more completely hidden than the cocoons of the Puss and Kitten moths formed upon bark and entirely covered with fragments of bark. They have all the colour, texture, and hardness of the bark of which they appear to be a part; yet they are often opened and the pupa extracted. There is little doubt that they are discovered by tree-creeping birds which tap the bark and detect the cocoon by its hollowness ("*Essays on Evolution*," Oxford, 1908, pp. 158, 159.)

Exposed pupae are often dimorphic, the two colours being those prevalent in their surroundings—the green of living leaves and the brown of dead leaves and bark. The chrysalises of the Geometrid genus *Zonosoma* (*Ephyra*) are good examples. So far as experiments have gone there appears to be no power of individual colour adjustment in these species, but further work with larger numbers is required in order to test this conclusion. Even in the absence of such a power the dimorphism is of advantage, giving the enemy a more extensive field over which to search. Furthermore, both of the tints are so universal in nature and so intermingled, that green upon brown or brown upon green is easily passed over. These pupae are suspended like those of many butterflies by silken threads at the tail and a girdle round the middle. The green pupae are produced from green larvae, the brown from brown, a condition not hitherto found in any other genus so far as I am aware.

Dimorphism and still more polymorphism become a far more efficient protection when they are associated with susceptibility, so that the colour of the surroundings gives rise to a stimulus which evokes the same colour in the insect. This has been known for a long time in caterpillars, a good example being those of the common Peppered Moth (*Amphidasis betularia*), which may be made green, various shades of brown (darkening into black in extreme forms), and even white, by intermixing with the foodplant various objects such as dead leaves, twigs of various tints and white paper spills. The changes take place in larvae reared from the eggs of the same female. All the results are such as may be seen in nature; for even the white larvae may be found on plants with glaucous or woolly stems or twigs. The use of sky-blue or scarlet objects does not produce any corresponding effect, but only some one of the appearances well-known in the wild caterpillars.

Mr. T. W. Wood was the first to show, in 1867, that the pupae of the Common Garden White butterflies were dark on dark surfaces, light on light ones, and at any rate sometimes green upon green leaves (*Proc. Ent. Soc.*, 1867, p. xcix.). These observations were confirmed by Prof. Meldola in 1873 (*P.Z.S.*, p. 153) and in the following year, Mrs. M. E. Barber showed that the pupae of the African *Papilio nireus*, were deep green upon the green twigs and among the leaves of the Orange-tree, pale green among withered yellowish-green leaves on a dead branch of *Vepris*, pale and wood-like when attached to the wooden frame of their cage (*Trans. Ent. Soc.*, 1874, p. 519.).

At the time when these experiments were made, it was believed that the moist surface of the freshly exposed chrysalis was, as it were, photographically sensitive to the light rays reflected from surrounding surfaces and that the harmonious colour was thus directly evoked. But in 1886, I was able to show, by experiments on the Peacock and Small Tortoiseshell, that the colour of the pupae is really determined in a period of many hours during which the caterpillar rests upon or is attached to the surface on which it will pupate. The Peacock pupae were in this way rendered dark or a beautiful golden green and the latter appearance was produced in the dark and against black surroundings if the caterpillar had been exposed on a bright surface during the sensitive period. Tortoiseshell and Red Admiral pupae became either dark or glittering with a metallic lustre like polished gold, sometimes over the whole surface, sometimes in patches (*Phil. Trans.*, Vol. 178 (1887) B. p. 311).

Special experiments were devised in order to test whether the stimulus determining the pupal colour was received by the eyes or the skin of the caterpillar. Larvae of the Small Tortoiseshell were enclosed in tubes each of which was gilt-lined for half its length and black-lined for the other half, and it was found that the anterior half of the caterpillar (which of course includes the eyes) was no more effective in producing the pupal colour than the posterior half. The extent of skin surface exposed to the reflected light rays appeared to be the essential cause. Furthermore, although each tube was of two colours the pupae were of one intermediate tint all over, a result which leads to the conclusion that the nervous system is involved and that the conflicting stimuli meet and counteract each other in some centre from which emerges a resultant impulse producing the uniform tint.

Colour susceptibility of the kind described above is common in butterfly pupae, but almost unknown in moths. There is however one species, the well-known Swallow-tailed Moth (*Uropteryx sambucaria*), in which the pupa is dark brown or pale yellowish, according to the colour of the surroundings. The caterpillar spins a very loose and open network in which the pupa is exposed to sight so that the power of colour adjustment is doubtless of much value to the species. Many experiments on the larvae and pupae of this species were made by Miss Bridges in 1909 and 1910 (*Trans. Ent. Soc.*, 1911, p. 136).

The persistence of the larval colours into the pupal stage of *Zonosoma* (*Ephyra*) was spoken of on p. 73. An even more remarkable instance of such persistence has been carefully investigated by Mr. John H. Gerould, who has shown that the blue-green caterpillars of the North American *Colias philodice* produced blue-green pupae and butterflies with blue-green eyes, whereas the pupae and eyes were yellowish grass-green, when the caterpillars were of this, the usual colour. Furthermore the empty pupal shell and the eggs were pure white when the larvae were blue-green as compared with golden yellow and cream respectively, when the larvae were grass-green. The Braconid parasites spun white cocoons when they emerged from blue-green larvae, golden yellow when from grass-green (See *Proc. Ent. Soc.*, 1922, p. vi., for abstract and reference). There is no doubt that these results are not due to any colour susceptibility, but to a true dimorphism which is inherited according to Mendelian laws, the bluish tint being recessive, the yellowish dominant. The two forms of larva differ in that one can utilise as a colour only the blue-green constituent of its foodplant, while the other can also utilise the yellow constituent.

Cocoons are often coloured by a secretion of the larva, and experiments on a large scale are much wanted in order to test whether the tints are ever adjusted to the background. At one time this appeared to be true, but Prof. Bateson showed that disturbance of the larva affected the result, and accounted for the difference observed in the cocoons of the Small Eggar moth (*Eriogaster lanestris*). It is important in experiments of this kind to touch and move the caterpillar as little as possible. White paper, with pale silver sand or fragments of chalk, would make a good background of one kind, and peat, with dark stems of the heather, a favourable contrast. The caterpillar of the Emperor moth (*Saturnia carpini*) would be an excellent subject for experiment, but care should be taken to prevent interference due to crowding; indeed the most trustworthy results would be obtained with single caterpillars each in its own box or compartment. The light and dark backgrounds should be freely and equally illuminated. Another common and favourable species is the Green Silver Lines (*Halias prasinana*), but here dead leaves should be employed for the dark background and a third surface should be provided with green leaves in order to test whether green which in nature will become brown produces the same effect as brown itself.

Exceedingly interesting modifications of the cocoon-building instinct were discovered by W. A. Lamborn in S. Nigeria. In one of these, the caterpillar of a little moth, *Euproctis lanaria*, allied to our Goldtail (*Porthesia similis*), spins a thin-walled balloon-like structure and then itself retires into the thick silken floor and becomes a pupa. The appearance is that of an empty cocoon (*Proc. Ent. Soc.*, 1913, p. v.). Another of Lamborn's discoveries is still more remarkable. Everyone must be familiar with the dead and dried-up bodies of the Large Garden White caterpillars, adhering to walls and tree-trunks in the autumn, and covered with the little yellow oval cocoons of Braconid parasites which have devoured the larva. These cocoons are very tough and each encloses only a small fraction of the nutriment contained in a caterpillar. Therefore a caterpillar or chrysalis devoured by Braconid larvae is of little use to an insect-eating enemy; and Lamborn found that an African caterpillar allied to our Scarlet Tiger (*Callimorpha dominula*), covers its own cocoon with sham Bracon cocoons. As the larvae spins it ejects, every now and then, a little mass of froth which it drags off by silken threads spun round it and then attaches to the cocoon by the same means. Each mass hardens into a yellow sphere so like a parasitic cocoon that for some time this keen observer was quite taken in by them (*Proc. Ent. Soc.*, 1911, pp. xlvi., liv., xcvi.).

A similar deception is practised by a little Indian moth *Epicephala chalybacma* belonging to the group which includes our Clothes-moths. The caterpillar, after spinning a cocoon on the underside of a leaf, ejects a minute sphere of white froth. It then turns round in its cocoon, bites a hole in the wall and pushes the sphere to the outside, anchoring it by a girdle of silk and a cable secured to the inside. It then ejects another sphere at the opposite end, turns round again and treats it like the first. Thus a mass of white pearl-like spheres is collected at each end of the cocoon and gradually advances until it meets the mass from the opposite end. The chrysalis is thus concealed by an opaque covering which suggests a cluster of the eggs of some insect or spider. This most elaborate and surprising instinct was discovered by Mr. E. E. Green in Ceylon (*Proc. Ent. Soc.*, 1912, p. cvi.).

Other examples of adaptation in cocoon-building, explained and shown upon the screen, are described in the address delivered at Reading in 1921 (*Trans. S.E. Union. Sci. Societies*, 1921, p. l.), and it is not necessary to repeat the descriptions in this abstract.

In conclusion I wish to bring forward an example of which the interpretation is still uncertain—the flattened oval cocoon of a Noctuid moth (*Labanda fasciata*) from Ceylon, bearing on the most prominent part of its surface a long and wide aperture through which the pupa is clearly seen. It is not the orifice by which the moth emerges. This is at one end and is also open from the first. The prominent opening is carefully constructed with an inturned margin, so that the visible edge is beautifully rounded. It is quite unlike the hole through which a parasite gnaws its way out, and I can only suggest that the appearance resembles some vegetable structure such as a seed lying in its capsule or a peculiar gall or fungus. The meaning can only be discovered in nature, but the structure bears such evidence of adaptation that I have no doubt that it is an example of protective resemblance. This very interesting and puzzling cocoon, which we owe to Mr. E. E. Green, is described and figured in *Proc. Ent. Soc.*, 1924, p. xx.

I have attempted in these few examples briefly described, to show some of the special adaptations by which butterflies and moths are enabled to surmount the special dangers of pupal life.