

Why do adult insects not moult?

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Hypotheses are presented concerning why mayflies moult after functional wings develop and why most insects cease to moult at this time. The pattern of retention or loss of the subimaginal moult in extant mayflies suggests that this moult may be necessary to complete elongation of caudal filaments and forelegs of adults. It is then analogous to the pupal moult of holometabolous insects. I propose that selection for wing efficiency has normally confined the presence of functional wings to one instar only, which is also the last and reproductive stage. Selection for light wings has generally caused the epidermis of membranous insect wings to degenerate, thereby precluding otherwise advantageous adult moults.

KEY WORDS:—mayflies—subimaginal moult—wing efficiency.

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INTRODUCTION

Mayflies (Ephemeroptera) are the only extant insects which moult after functional wings develop. The first winged instar (subimago) flies from the shed nymphal skin, left on the water's surface, to nearby vegetation, where it remains briefly until it moults to the adult instar (imago). A functional explanation of the subimaginal stage has not yet been presented; in fact, it has been considered a nonadaptive relict trait (Snodgrass, 1954; Schaefer, 1975). The double moult between nymph and reproductive adult in mayflies raises the more general question of why other winged insects do not moult after functional wings are acquired at reproductive maturity and why functional wings are confined to the last instar. In this paper I present hypotheses about the significance of the mayfly double moult and the more general problem of why insects usually do not moult as adults.

THE SIGNIFICANCE OF THE MAYFLY IMAGINAL MOULT

A possible explanation for the adaptive significance of the unique subimaginal moult of mayflies derives from the changes that occur during the moult and the pattern of moulting in the order.

Because the subimago does not feed there is no overall growth in body size during this instar. The transition to the subimago, however, involves several changes in body form. These include increase in length of the legs, particularly of the forelegs, and of the caudal filaments, and completion of the genital structures and the large compound eyes of males (Needham, Traver & Hsu, 1935).

The forelegs and caudal filaments of adult mayflies are usually much longer than those of the nymph. Some crude approximations extracted from data in Eaton (1883–1888) and Needham *et al.* (1935) indicate that the forelegs of the adult may be as much as four times that of the nymph and the caudal filaments as much as ten times. Most of the elongation in the forelegs is achieved through growth of the tarsus, which may be more than ten times the length of that of the nymph.

Because of the relatively inelastic nature of the exoskeleton of arthropods, there is a low limit to the amount of size increase at each moult. Enders (1976) reports that the usual growth increment between arthropod moults in a linear dimension ranges from 20% to 60%. This means that the new structure is generally less than twice the length of the old. Since this observed range is similar to size differences found among sympatric congeners and among immature age classes in other organisms, it may not represent the mechanically maximum size increase between moults but may be related in part to ecological considerations (Enders, 1976; Horn & May, 1977; Maiorana, 1978). Attention has not been paid to the maximal increment that can occur between moults, particularly in well-sclerotized structures such as legs. Some arthropods with a thin article can increase many times their initial size without moulting but this process of neosomy does not involve the appendages (Audy, Radousky & Vercammen-Grandjean, 1972). Savory (1964) reports that arthropods which have lost appendages generally require several moults to regenerate the entire appendage.

The evidence on the usual growth per moult suggests that there is a limit to how much an appendage can elongate in a single moult, and that this limit is below the typical amount of elongation in appendages between the nymphal and adult mayfly. If this is demonstrated to be the case, it may be an adequate explanation of the subimaginal moult in mayflies. The abrupt and tremendous elongation of the forelegs and caudal filaments between the nymphal and adult stage may require two moults to complete.

The long forelegs and caudal filaments are reproductive adaptations of mayflies (Needham *et al.*, 1935). The adult is strictly a reproductive stage and even lacks functional mouth parts. The adult generally lives for only a day and rarely more than several days. Mayflies have a unique courtship dance during which the male flies under the female and holds on to her thorax with his long forelegs, which he suspends directly above himself. The long caudal filaments aid in the balance of the insect during flight. The female forelegs are not as exaggerated as the male's but they also are typically much elongated over that of the nymph.

The usually bottom-dwelling or burrowing aquatic nymph would likely find such elongate structures awkward and perhaps even dangerous to their mobility.

In fact, in many nymphs the hind legs are often longer than the forelegs (Eaton, 1883–1888). I suggest that the unique reproductive adaptations of the adult require a form that cannot be acquired gradually during the nymphal stage. This abrupt transition in form has necessitated an additional moult between the final nymphal and adult stage.

Qualitative support for this hypothesis comes from the pattern of moulting in the order. In some genera only the males undergo an imaginal moult. These are *Ephoron*, *Campsurus* and *Palingenia* (Spieth, 1940). The males have relatively long forelegs but the other two pairs are reduced in length and functionless. They also have long caudal filaments. In females, which forego the subimaginal moult, we expect and find that all three pairs of legs are quite reduced in length, as are their caudal filaments. In one species, *Plethogenesia papuana*, neither male nor female undergoes the subimaginal moult. In both sexes all three legs are reduced and functionless, and the caudal filaments are relatively short. Mating in this species is unusual, occurring on the surface of the water rather than in flight (Eaton, 1883–1888).

The hypothesis I propose to explain the subimaginal moult in mayflies is similar to that proposed by Hinton (1963) for the necessity of a pupal instar in endopterygotes. He argues that the evagination and subsequent growth of wings cannot be completed in one moult. Unlike those of exopterygotes, the wings of endopterygotes cannot begin enlarging until they have evaginated at the larval-pupal apolysis because, during the larval period, muscles in the thorax prevent the wing discs from increasing in size. In mayflies the long adult legs are presumably disadvantageous to the nymph, as discussed above. Consequently, the legs do not begin elongation until the moult from nymph to subimago. Another moult is then required to complete their development.

All other insects with long appendages restricted to the adult are holometabolous. They reconstruct their body during the pupal stage and so are freed from the constraint of elongating a structure within a shorter cuticle.

The elongation of legs in a second adult moult, rather than in an abbreviated last nymphal moult, may have been selected for early in the evolution of mayflies when predation on nymphs in the aquatic environment may have been more intense than that occurring in the aerial environment. Among extant mayflies there is an evolutionary trend towards reduction in length of adult life. This reduction is correlated with setting the timing of the imaginal ecdysis back until it nearly coincides with the last nymphal ecdysis. Discarding the moult entirely is the extreme expression of this trend, although it may be associated with burrowing adaptations of the nymph. Those groups in which the second moult is dropped in part or entirely have nymphs which burrow in the substrate. These nymphs are characterized by relatively short legs and caudal filaments. Perhaps in these groups attainment of the long legs that may be needed for the mating dance cannot be achieved easily or even in two moults. Possibly then a new mating system evolved. The reduction in adult life span of mayflies may have been the result of the evolution and radiation of birds.

THE SIGNIFICANCE OF NOT MOULTING AS ADULTS

Many terrestrial arthropods, including primitively wingless insects, continue to moult after reaching maturity (Snodgrass, 1954). The advantages of subsequent

moult include continued growth, which often enhances reproductive output, and the ability to regenerate lost appendages. Presumably many insects should benefit from the advantages of continued moulting unless drawbacks unique to insects outweigh them. Such drawbacks probably involve wings, since these are a unique feature of insects not possessed by arthropods that moult after maturity.

Snodgrass (1954) suggested that extracting large membranous wings from the old cuticle is hazardous because they can readily be torn. Therefore winged insects cease to moult once they acquire functional wings. His hypothesis also suggests an explanation for the lack of functional wings in preadult instars: the wings remain relatively small so as to reduce the danger of tearing them during the moult. Whether wings are more susceptible to injury during moult than other delicate structures, such as antennae, has not been directly tested.

The subimaginal moult of mayflies poses a problem for his hypothesis: since mayflies have a complex mating flight that is essential for copulation (Needham *et al.*, 1935), wings are essential to their reproductive success. Thus, in this insect group in particular, selection should have eliminated any unnecessary moults if such moults are likely to damage the wings. His suggestion then that the subimaginal moult in mayflies is a nonadaptive trait of a primitive insect group seems inconsistent with his hypothesis.

An alternative hypothesis explaining confinement of functional wings to one instar is that selection for wing efficiency caused degeneration of the living epidermis in the wings and hence suppression of subsequent moults. This hypothesis does not exclude that of Snodgrass and in fact both selective factors may have been involved.

The efficiency of insect wings is increased if strengthening and lightening of wings can be achieved simultaneously (Forbes, 1943; Edmunds & Traver, 1954; Rees, 1975). Increasing the amount of sclerotization of the cuticle strengthens the wing but produces a heavier wing. The first winged insects are thought to have had this type of wing but no direct evidence supporting it exists in the fossil record (Edmunds & Traver, 1954; Hamilton, 1971). The Devonian fossil *Eopterum devonicum*, thought to represent this stage in the evolution of winged insects, has been shown to be part of the leg of a crustacean (Rodendorf, 1972).

Most fossil and extant insects have strengthened their functional flight wings by increasing sclerotization of veins and decreasing that of the region between veins. Wings can be further lightened by degeneration of the living epidermal tissue, which has a high water content. In fact this often happens in the membrane portion of wings (Snodgrass, 1935; Waddington, 1940).

I propose that it is this loss of living epidermis that selects against subsequent moulting. Since the epidermis secretes the new cuticle, the wing cannot moult once the epidermis degenerates. Although it is possible that the water content of the epidermal cells can decrease without permanent cell degeneration, even if this is the case, cells would have to regain this water before they can be functional and secrete a new cuticle. Thus, in order to moult, wings have to undergo a stage of lower flight efficiency while a new cuticle is being formed. According to Needham *et al.* (1935), the subimaginal stage of mayflies is a quiescent one. Except for its initial flight from the water, the subimago rarely flies unless disturbed and does not seem efficient in flight. Because it sheds the cuticle of its wings in the imaginal moult, (Taylor & Richards, 1963) the subimago must retain living epidermis in its wings until the new cuticle is formed.

Secondarily wingless insects, even those which have been wingless for a long time (lice and fleas) do not moult after reproductive maturity. In order to regain the ability to moult these insects would have to modify their hormonal system (Wigglesworth, 1954). This may not be simple developmentally and hence only very strong selective pressures for continued growth would result in a change. Presumably the advantages of continued growth have not been sufficient in these insects. Alternatively, since lice and fleas are ectoparasites, there might be some adaptive upper limit to body size.

Fossil evidence suggests that some Paleozoic insects had at least two or three instars with functional wings. Whether all instars were reproductive is not known. But then the subimago of the mayfly is not a reproductive stage. The Paleozoic paleopterous order Palaeodictyoptera may have had at least one moult between instars with fully developed wings, based on a record of a shed cuticle of an ovipositor attached to a female *Lycocercus goldenbergi* (Kukalova-Peck, 1975). Kukalova-Peck suggests that the descendent order Megasecoptera may also have had such a moult. More convincingly, Sharov (1957) claimed that an early Permian species (*Atactophlebia termidoides*), which he referred to his now extinct orthopteroid order Paraplecoptera, had two moults between instars with functional wings. Since the fossils were only wing impressions it is unknown whether the stages were mature. The 17 wings fell into three size groups, the two smallest of which indicated a high water and organic content, less distinct veins, and in general, less aerodynamic efficiency. The largest wings were membranous and seemed most efficient. Summarizing the available fossil evidence, Kukalova-Peck (1978) concludes that all major groups of Paleozoic insects had several instars with functional wings, but it remains uncertain whether moulting continued after sexual maturity.

The now sharp demarcation between the flightless nymphs and efficiently flying adult of hemimetabolous insects may have been the result of disadvantages associated with large membranous but not particularly efficient wings. Only in mayflies, which need an extraordinary elongation of appendages during the transition between nymph and adult, has more than one stage with functional wings been retained. And the subimago rarely lasts long and does not involve activity other than flying from the aquatic nymphal environment to a branch along the shore, to await the final moult before engaging in a brief courtship dance.

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