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SHORT COMMUNICATIONS

THE PROCESS OF MOULTING DURING FINAL EMERGENCE OF THE DRAGONFLY *PANTALA FLAVESCENS* (FABRICIUS) (ANISOPTERA: LIBELLULIDAE)

R.J. ANDREW and N. PATANKAR
Department of Zoology, Hislop College, Civil lines, Nagpur-440 001, India
rajuandrew@yahoo.com

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The chain of events occurring during emergence in *P. flavescens* is described in detail. The moulting process is divided into 3 stages. The larva climbs out of the water a few hours after sunset. If disturbed while climbing, it exhibits thanatosis i.e. death feigning and crab-like side-ways crawling. It stops at a suitable vertical emergent support. Manipulation from vertical to horizontal of this support stops commencement of ecdysis. – Stage I starts from the moment the larva finds a suitable site for moulting. Soon, it starts shuddering, quivering and shaking its body in a synchronized pattern. The imago inside the exuviae exerts pressure on the thoracic tergites until the cuticle splits. This stage varies from 8 to 20 min and occupies 16% of the moulting period. – During stage II, the head and thorax of the imago emerge out of the split thoracic cuticle. The imago exhibits an antero-posterior humping movement and the body hangs out downwards with folded legs. The half suspended, upturned imago starts 'breathing' heavily. Unfolding of the legs and movements of the packed wings takes place in a characteristic manner. The imago turns upwards, grips the head of the exuviae and jerks out the remaining terminal portion of the abdomen from the exuviae. This stage takes 18 to 35 min and occupies 31% of the moulting time. Pigmentation of the head region is completed during this stage. – In stage III, the imago is released from the exuviae, it starts hardening its cuticle and extending the wings. The imago moves a few inches above the exuviae. The abdomen is pale green and curved upwards. The wings expand but are opaque. Simultaneously, pigmentation of the body starts around the thoracic region and the terminal tip of the abdomen. Within 10-14 min the whole body of the imago develops a species-specific teneral pattern of colouration. Meanwhile, the expanding wings unfold and separate out and the teneral adult is ready for flight. This stage takes 40-55 min and occupies 53% of the total moulting period. Observations on incomplete metamorphosis indicate that gravitational force is responsible for uniform wing expansion.

INTRODUCTION

Moulting during final emergence, or final metamorphosis, is one of the most spectacular events in the life history of a dragonfly (MILLER, 1995). This process has been observed and discussed by various workers (TILLYARD, 1917; CORBET, 1951; PAJUNEN, 1962; TROTTIER, 1966; BULIMAR, 1971). Moulting is a highly complex process in which many different types of rhythmic movements participate.

CORBET (1999) noted that it was not easy to determine stage I and stage IV of metamorphosis in Odonata, The larvae of many species leave the water partly or wholly and intermittently, days or even weeks before emergence and it is not easy to time stage IV in Odonata because various extrinsic factors like dawn, twilight and temperature and even endothermic warming control the first flight, which concludes stage IV.

MATERIAL AND METHODS

The city of Nagpur (21°10' N / 79°12' E) lies at the southern fringe of the Satpuda mountain range in central India. It is located on an undulating plateau with altitude ranging between 274-305 m above mean sea level. The collection site was a 15 m long stretch of a 120 m long open cement drain running in a west-east direction. It has a width of 34 inches and a depth of 32 inches. Depth of water of about 5 inches accumulates at the bottom due to the presence of a single brick layer placed across the floor of the drain. The drain is located at the large grass covered playground surrounded by shrubs and few trees of the St John's School in the centre of the city.

Mature F-0 larvae were collected from this site and kept in buckets and plastic containers, partially filled with the water from where they were collected. Wooden sticks, twigs and branches were placed in the containers as emergence supports. Natural conditions were maintained by keeping the containers in a veranda, near large open windows. With the help of an aim-n-shoot 35 mm Yashica camera (model: EZX-105, 38/105 mm) the various stages of the process of moulting during final metamorphosis were photographed.

All the movements of the larva/emerging pharate were documented and a Nokia 1100 cell phone's stopwatch was used to record the time (one of the major merit of using this cell phone was the inbuilt tiny cool torch which was of great help during the recording of observations in the dark).

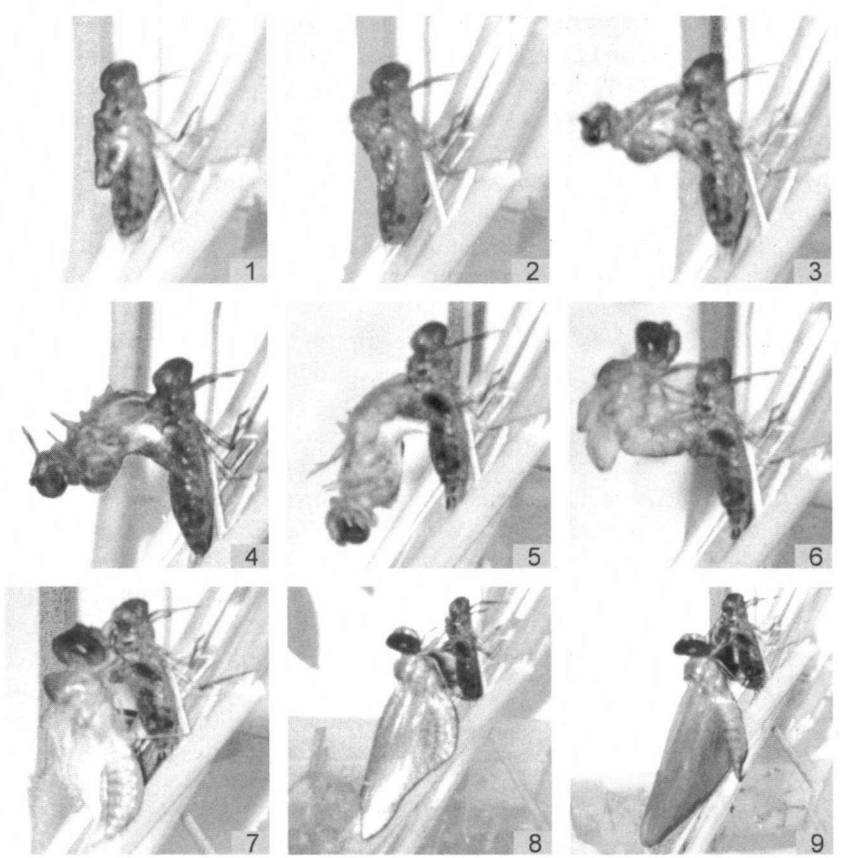
RESULTS

The following documentation is of one complete session of moulting during the final emergence of *Pantala flavescens*, which was observed on the night of 15th April 2004.

The larva rested with its head and thorax out of water since early evening (6:25 pm.). At 11:10 pm, it moved out of the water and climbed 13 inches, stopping at a suitable emergent support (dried branches, stick).

Stage I (Figs 1-2). – After a rest of 96 seconds, the larva started jerking its head sideways 'left and right'19 times. Then it pushed the head and thorax

upwards seven times with legs spread and the posterior region of the abdomen firmly pressed against the base. The larva moved the head sideways twice and curved up the abdominal tip once. It reset the grip of its legs and pushed up the head and thorax but the abdomen lay pressed against the base. The head moved sideways eight times, slowly rising with every move (as if taking a deep breath). It re-gripped and repositioned its legs and slightly elevated the thorax. The fore-legs started twitching, while the hind legs re-positioned themselves. The fore legs started quivering without losing their grip. At this stage, the terminal end of the abdomen was firmly pressed against the base. The head lifted and the fore legs displayed clawing movements which stopped after eight seconds. The head and thorax jerked up and down 14 times. The right wing pad elevated slightly in six tiny jerks but returned to its original position. A dark split appeared in between the wing pads. This stage concluded at 11:35 pm.



Figs 1-9. *Pantala flavescens*, final metamorphosis: (1-2) stage I; – (3-6) stage II; – (7-9) stage III.

Stage II (Figs 3-6). – The larva remains motionless but the right wing buds exhibited slight lateral movement which stopped after 28 seconds and the larva again became motionless.

At 11:40 pm the wing buds rose while the thorax lifted. The head and thorax of the adult emerged out of the split. Initially, the thorax emerged, followed by the head. It did not wriggle but moved up and down. By 11:45 pm the head and thorax hung out and jerked once. The abdomen of the adult lay trapped in the exuviae of the larva. The legs, which were folded against the thorax, started twitching but in a folded position. The body of the adult hanging out expanded and relaxed as if 'breathing' heavily. It started an antero-posterior conspicuous 'humping' movement, trying to loosen its skin from the larval exuviae. The body of the pharate was filled with haemolymph and appeared green. The legs were still folded against the thorax but now they started moving. The first pair of legs was folded but started to jerk at the tibia-femur joint. The joint moved up and down along the neck region. The folded legs started jerking at a rate of 2-3 jerks per second. The second pair of legs unfolded (just the angle of femur and tibia increased from 10 to 40 degrees around the neck). The 1st and 2nd pairs of legs started twitching. The twitching intensity of the 1st pair of legs was much higher then the 2nd pair. The hind wing pads, which initially lay parallel to the body, now hung outwards and downwards perpendicular to the abdomen. The forewings lay parallel and close to the abdomen. The pharate turned upward, gripped the head of the exuviae and at the same time pulled out the abdominal tip from the exuviae, ending stage II of metamorphosis at 12:06 am.

Stage III (Figs 7-9). – The pharate gripped the head of the exuviae with the 1st and 2nd pair of legs. The 2nd pair gripped firmly but the 1st pair tried to get a better hold by re-gripping the head. The 3rd pair of legs hung down without touching any substrate. The abdomen and wings started to stretch. By 12:18 am, the opaque white wings were completely stretched but still stuck to each other, while the abdomen was still curved but by 12:24 am, the abdomen was completely elongated, straight and started to sclerotize. Simultaneously, the wings stretched out completely and became transparent. Pigmentation of the body started from the thorax and the terminal tip of the abdomen (the head was already pigmented by the end of stage II). The teneral moved 2.5 inches above the exuviae. After forty minutes since turning upward, by 12:36 am, the wings became unstuck from each other, separated and now lay perpendicular to the body.

Table I

Pantala flavescens: the duration (minutes) of the three stages of the final metamorphosis in three observed moultings

Specimen	Stage I	Stage II	Stage III	Total
1	12	18	42	72
2	20	25	55	100
3	08	37	40	85
Average %	16%	31%	53%	100%

The abdomen became completely sclerotized and was coloured with its species--specific pattern. This ended stage III of metamorphosis.

The time duration of the three stages for three observed final ecdysis is illustrated in Table I.

THANATOSIS

One larva was resting on the outer surface of the bucket, we caught it and placed it horizontally on the rim so that the body was parallel to the ground. It stiffened and straightened all three pairs of legs along the side of its abdomen and dropped outside on the ground. For more then 15 seconds, it exhibited thanatosis (acted dead), then darted quickly up the side of the bucket and, after climbing up only three inches, it quickly started the process of eclosion within four minutes. It was 11:45 pm. The main survival value of this thanatosis behaviour is probably to avoid further attack by a large predator. The emerging larva of *P. flavescens* is prone to attack from land predators and it is only physical stimuli that can excite this behaviour since moulting takes place in darkness. ARAI (1987) reported that thanatosis or reflex immobilization can occur shortly before ecdysis and before emergence. It is strongly exhibited if the larva is grasped by the thorax out of water, thus responding to physical stimuli rather than visual as found in the present study. The haste to moult almost immediately after exhibiting thanatosis behaviour in *P. flavescens* should be noted as a survival instinct as found in *Hemigomphus heteroclitus*, which completed ecdysis within 10 minutes before an impending storm (TILLYARD, 1917). At 2:00 am, a completely sclerotized, motionless adult was resting on the exuviae, legs clutching the exuviae head.

Generally we find that the pharate adult, just after final ecdysis, is found a few inches above its exuviae. Since extra energy was spent before moulting (in pretending thanatosis), it may be possible that now the pharate has no energy left to move a few inches above the exuviae as noted in normal circumstances. At 6:00 am, we gently carried the bucket out; the adult flew upwards (18-20 inches) and darted away towards the East.

ANGLE OF ECDYSIS

Aeshna juncea can complete ecdysis at 0 degree (vertical) (MAITLAND, 1967) whereas *Stylurus annulatus* can be forced to emerge at 180 degrees on a mesh net. *Orthetrum albistylum speciosum* could not do so at 0 degree (INOUE, 1964). HEYMER (1972) found that a *Calopteryx* larva tried to regain its vertical position when the angle of the vertical substrate was manipulated. Inverted emergence occurs in *Xanthocnemis sinclairi* and three species of *Ischnura* (ROWE, 1987; CORBET, 1999) while horizontal emergence is common in Zygoptera and

Gomphidae. We manipulated the position of a larva ready for ecdysis from vertical to horizontal by placing it on a flat surface but the larva did not moult but always re-oriented itself in the vertical position, by darting quickly towards an erect vertical substrate. If a physical obstacle was kept in its path, it moved sideways crab-like, without changing the orientation of its body. As far as is known this is the first time that such crab-like side-ways locomotion of a mature odonate larva on land has been reported.

PHARATE TRAPPED AT STAGE II

On 11th April 2004 at 10:40 pm, one pharate adult was found hanging down from its exuviae. It tried desperately to arch upwards so as to catch the head of the exuviae and release itself, but could not succeed. It hung down, legs thrashing, but it could only turn up half-way and then fell back to its hanging position.

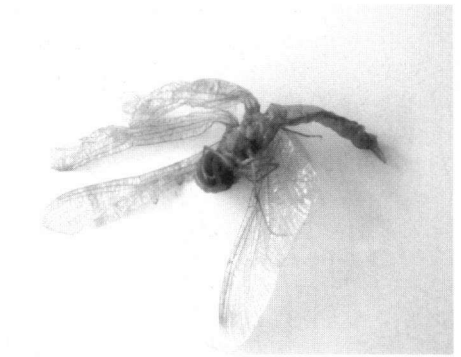


Fig. 10. *Pantala flavescens*: pharate trapped at stage II. – Note the forwardly directed wings and the uneven stretching of the wings on the left- compared to the right side.

Soon, the wings started expanding in the hanging position and 90% of the wings spread lengthwise but pointing downwards. It stayed in this position for more than 30 minutes. Then it again tried to up-right its position and, after four attempts, it caught hold of the emergent support towards the left of the exuviae but could not proceed further to regain the natural symmetrical position. It held this position with the abdominal tip still trapped in the exuviae. The wings continued stretching even while the imago was held immovable in this lopsided position. Within ten minutes, the wings hardened and were now pointing upwards. The pharate was still struggling to remove its trapped abdominal tip from the exuviae but could not succeed. Later, at 2:00 am, we found the pharate floating on the water surface with its abdomen almost stretched and tanned and with its wings pointing forward and exhibiting asymmetrical stretching. A close examination of the wings revealed that the fore- and hindwings of the right side had stretched more than the wings of the left side (Fig. 10).

DISCUSSION

EDA (1963) distinguished two types of posture during emergence, the upright type found in most Coenagrionidae, Gomphidae, Lestidae, Petaluridae, Platycne-

mididae and Pseudolestidae and the hanging type reported in Aeshnidae, Calopterygidae, Coruliidae, Epiophlebiidae, Libellulidae and sometimes in Petaluridae, and proposed that this reflected the larva's taxonomic position. In the upright type, the larva completes moulting with the angle of 0 degree between body and exuviae during stage II whereas in the hanging type as found in *P. flavescens* the angle is between 90-130 degrees. The other major difference is in the expansion of the wings, which in the upright type starts from the base whereas in the hanging type they expand uniformly.

CORBET (1999) noted that it was not easy to determine stage I and stage IV of metamorphosis in Odonata. The larvae of many species leave the water partly or wholly and intermittently, days or even weeks before emergence. They usually leave the water by climbing emergent vegetation or by walking onto the shore and, when emergence supports are few, some individuals walk up to 30 m to find an emergence support. Thus it is difficult to measure the time of stage I because it is directly dependent upon the distance and/or the presence of an available emergence support. The present paper proposes that the time period of stage I should therefore start from the time the larva finds a suitable spot for ecdysis rather than the time it leaves the water. Further it is proposed to end the process of metamorphosis in Odonata at stage III since, by the end of stage III, the individual has attained all the morphological characters of a pharate adult and

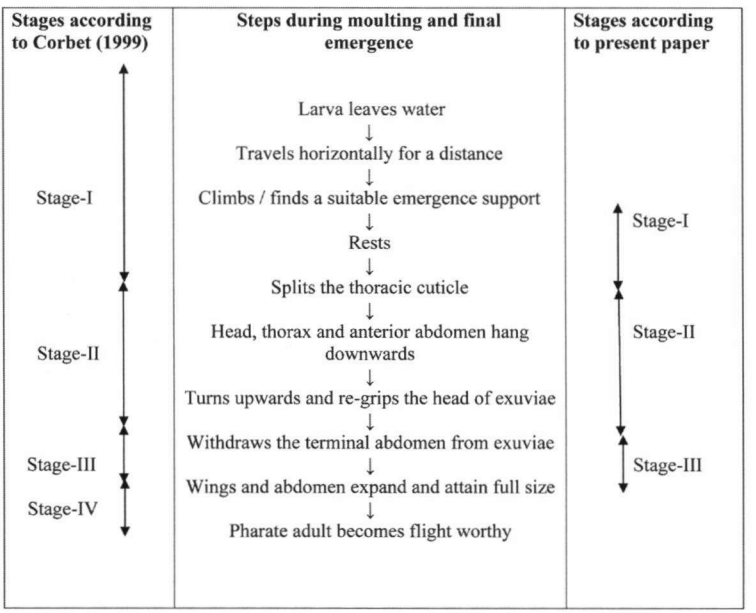


Fig. 11. Proposed stages of moulting during final emergence.

also because it is not easy to time stage IV in Odonata because various extrinsic factors like dawn, twilight, temperature and even endothermic warming control the first flight, which concludes stage IV (CORBET, 1999).

The changes proposed in the stages demarcated during the final moult of Odonata are compared and illustrated in Figure 11.

From the present observations of forwardly directed, asymmetrical stretching and spreading of the wings, it appears that gravitational force plays an important role in uniform wing expansion of dragonflies adopting the hanging type posture during emergence.

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