# A DROUGHT-RESISTANT LARVA OF PANTALA FLAVESCENS (FABRICIUS, 1798) (ODONATA: LIBELLULIDAE) IN THE LENÇOIS MARANHENSES, NE-BRAZIL

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*This paper is dedicated to Philip S. Corbet on the occasion of his 70th birthday.*

## Abstract

A single male of *Pantala flavescens* was collected by chance with dry mud in the bed of
a pond in the Lençóis Maranhenses (N-E Brazil) which had been dry for several months.
It was noticed as a larva in an aquarium about seven days after the mud first had been
wetted and it was then reared to the imaginal stage. Fifteen measurements were taken on
three larval skins that could be recovered. These were fitted to literature data on larval
development that had first been converted to exponential growth curves, in an effort to
determine whether the drought-resistant stage had been an egg or a larva. It was found that
that a drought-resistant egg was improbable, and that the larva had probably survived
drought as an early instar (2-4). It is argued that early larval tolerance to drought may be
common in *Pantala,* and may contribute as much to its success in semiarid environments
as its rapid larval development.


## Introduction

In December 1997, the first author made a field trip to the Lençóis Maranhenses (N-E Brazil)
to investigate the microscopic plankton fauna living in the numerous interdunar pools of
that tropical desert. There had been no rain for several months, and many dune lakes were
dry. Samples of dry mud were collected, to be incubated under laboratory conditions and
permit a study of the zooplankton that rapidly hatches from the stock of resting eggs
present in such sediments.
    One of the wetted mud samples yielded an animal of unexpected size, a male larva
of *Pantala flavescens* (Fabricius, 1798). The object of the present paper is to determine
the stage (egg or larva) at which dormancy in this larva may have occurred.

## Origin

The Lençóis Maranhenses in North-East Brazil (Maranhão state) is a vast (150 x 50 km) sand area, consisting of high transversal dunes. In the interdunal depressions, temporary waterbodies form during the rainy season (January-August). For more information about the region, see SEMATUR (1991).

The origin of our mud samples is a small (max. 1 km$^2$) temporary freshwater lake northwest of the village of Mandacaru (2°35'50" S, 42°42'46" W). Coordinates were determined *in situ*, with the help of a Global Positioner, type ENSIGN GPS.

## Material and methods

At the time of sampling, the lake bed was completely dry. Samples of dry mud were collected randomly from the upper 2 cm by hand. Crusts of dried filamentous algae and detritus were scooped up, together with empty gastropod shells (*Ampullaria* sp.) and transported in hermetically sealed plastic bags. The crusts were completely dry at the time of collection, at an outside temperature of over 40 °C, and a sediment temperature of over 60 °C.

One month later, back in the laboratory, the mud crusts and empty gastropod shells were placed in a 200 x 80 cm glass aquarium, filled with slightly alkaline water of low conductivity. The water was kept at a constant temperature of 30±1 °C, using an adjustable heater. Two TL-lamps provided light at a constant, high intensity, day and night. Submerged water plants were present. There was no oxygen supply and the water in the aquarium was not changed.

The *Pantala* larva initially fed on the protozoans, aquatic oligochaetes (*Pristina evelinae*), ostracods (young *Chlamydotheca* sp.) and chydorids (*Chydorus* sp.) that spontaneously hatched from the mud. Later, we fed it terrestrial oligochaetes (*Lumbricus terrestris*) and anostracans (mainly *Branchipus* sp.) *ad libitum*. Food was therefore not limiting. The animal was not disturbed or displaced during observations and the aquarium was inspected daily. Three exuviae could be recovered and the dates of moulting noted. The age of these three exuviae was, as a first approximation, noted in days from first incubation of the sediment. The exuvia, as well as the adult male that later emerged from it, were preserved in ethanol 70%.

Remaining mud samples, though not many, were checked for the possible presence of other specimens of *Pantala flavescens*, but none were found.

Size measurements were taken under a type S Wild stereomicroscope equipped with a *camera lucida*. Head, thorax, abdomen and limbs of the exuviae were drawn and measured to the nearest 0.01 mm as shown in Fig 1. The 15 features measured are the same as those used by Lamb (1923, 1925). Only total length was not used, because of the possibility of non-negligible errors by extension of the exuvia.

Our biometrical data of the exuviae were fitted to the detailed measurements of Lamb (1923, 1925) (see Table 1), and combined with the information of Kumar (1984) on instar duration (see Table 2), who reared his larvae at a temperature-interval close to ours (28-32 °C). Assuming that we could fit our data to Lamb's, we first converted hers to
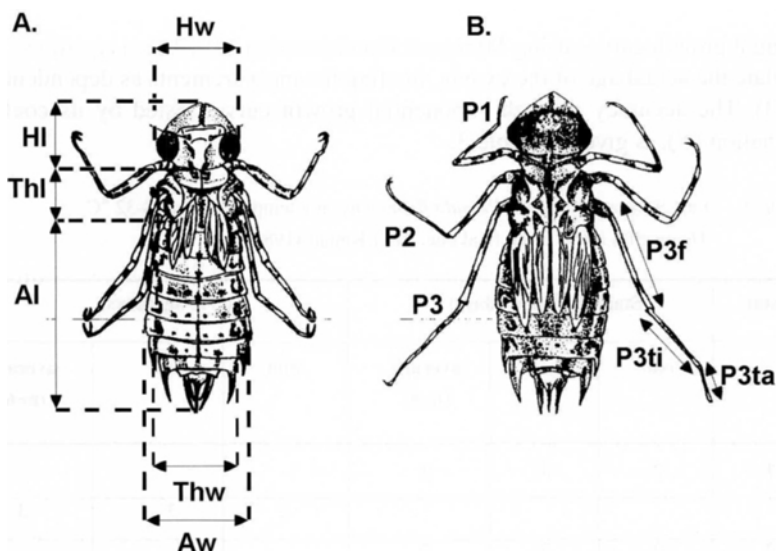
Figure 1. Biometrical measurements of larval *Pantala flavescens*. A. penultimate-instar larva; B. final-instar larva. Abbreviations: Al: length of abdomen; Aw: width of abdomen; Hl: length of head; Hw: width of head; P1-P3: first to third thoracic; P3f: length of third limb's femur; P3tib: length of tibia; P3ta: length of tarsus; Thl: length of thorax; Thw: width of thorax.

Table 1.    Growth in successive larval instars (1-12) of *Pantala flavescens*, the twelfth being the final one. All measurements in mm. Variables after Lamb (1923). For abbreviations, see Fig. 1.

| Instar | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Hw | 0.364 | 0.522 | 0.69 | 0.568 | 1.537 | 1.776 | 2.4 | 2.568 | 3.678 | 3.84 | | 6.5 |
| Hl | 0.264 | 0.378 | 0.492 | 0.616 | 0.852 | 1.032 | 1.344 | 1.704 | 2.04 | 2.4 | | 3.66 |
| $P_1f$ | 0.264 | 0.312 | 0.288 | 0.576 | 0.72 | 1.56 | 0.96 | 1.44 | 1.92 | 2.324 | | 5 |
| $P_1ti$ | 0.288 | 0.36 | 0.432 | 0.552 | 0.576 | 1.248 | 1.008 | 1.728 | 2.04 | 2.856 | | 4.5 |
| $P_1ta$ | 0.216 | 0.216 | 0.288 | 0.288 | 0.432 | 0.672 | 0.768 | | 1.2 | 1.596 | | 2.5 |
| $P_2f$ | 0.264 | 0.336 | 0.432 | 0.672 | 0.864 | 1.752 | 1.44 | 1.92 | 2.4 | 2.94 | | 6 |
| $P_2ti$ | 0.288 | 0.384 | 0.48 | 0.672 | 0.6 | 1.44 | 1.57 | 2.184 | 2.472 | 3.08 | | 5 |
| $P_2ta$ | 0.216 | 0.216 | 0.264 | 0.384 | 0.432 | 0.672 | 0.792 | 1.128 | 1.224 | 1.512 | | 2.5 |
| $P_3f$ | 0.312 | 0.388 | 0.624 | 0.768 | 1.032 | 1.8 | 1.8 | 2.64 | 3.246 | 3.976 | | 8 |
| $P_3ti$ | 0.312 | 0.432 | 0.576 | 0.768 | 0.752 | 1.68 | 1.57 | 2.352 | 2.88 | 3.64 | | 6 |
| $P_3ta$ | 0.216 | 0.336 | 0.24 | 0.432 | 0.504 | 0.768 | 0.792 | | 1.368 | 1.624 | | 2.5 |
| Thl | 0.318 | 0.371 | 0.438 | 0.608 | 0.767 | 0.916 | 1.248 | 1.68 | 1.92 | 2.688 | | 5.2 |
| Thw | 0.3 | 0.384 | 0.45 | 0.568 | 0.768 | 1.296 | 1.68 | 2.068 | 3.24 | 3.12 | | 5.2 |
| Al | 0.798 | 1.044 | 1.281 | 1.632 | 2.262 | 2.952 | 4.738 | 4.776 | 6.72 | 8.976 | | 15.87 |
| Aw | 0.321 | 0.888 | 0.618 | 1.128 | 1.464 | 1.992 | 2.496 | 3.24 | 4.608 | 5.232 | | 8.6 |

exponential growth curves using Microsoft Excel (version 7.0). These equations were used to calculate the actual age of the exuvia, treating the measurements as dependent variables (Table 3). The accuracy of each exponential growth curve, tested by its coefficient of determination ($r^2$), is given in Table 3.

Table 2.   Larval instar and age of *Pantala flavescens*, at a temperature of 28-32 °C.
The twelfth instar is the final one. After Kumar (1984).

| instar | Stage duration (days) | | | larval age(days) | | |
|---|---|---|---|---|---|---|
| | min | max | average (n=6) | min | max | average (n=6) |
| **1** | 2 | 3 | **3** | | | |
| | | | | 2 | 3 | **3** |
| **2** | 2 | 3 | **2** | | | |
| | | | | 4 | 6 | **5** |
| **3** | 2 | 5 | **3** | | | |
| | | | | 6 | 10 | **8** |
| **4** | 2 | 6 | **4** | | | |
| | | | | 8 | 16 | **12** |
| **5** | 2 | 6 | **4** | | | |
| | | | | 14 | 21 | **16** |
| **6** | 3 | 10 | **5** | | | |
| | | | | 17 | 26 | **21** |
| **7** | 4 | 9 | **6** | | | |
| | | | | 22 | 31 | **27** |
| **8** | 2 | 8 | **5** | | | |
| | | | | 28 | 36 | **32** |
| **9** | 4 | 7 | **6** | | | |
| | | | | 34 | 40 | **38** |
| **10** | 4 | 9 | **6** | | | |
| | | | | 39 | 49 | **42** |
| **11** | 4 | 8 | **7** | | | |
| | | | | 45 | 55 | **49** |
| **12** | 6 | 12 | **9** | | | |
| | | | | 57 | 61 | **58** |

Table 3.   Calculation of the age of the exuviae (in days; $x_1$-$x_3$), inferred from data of Lamb (1923) and Kumar (1984); $y_i$ = length, $x_i$ = age.

| feature | size of exuviae (mm) | | | equations | estimated age (days) | | |
|---|---|---|---|---|---|---|---|
| | $y_1$ | $y_2$ | $y_3$ | y = | $x_1 = 39.75\ (\sim 40)$ | $x_2 = 45.05\ (\sim 45)$ | $x_3 = 52.22\ (\sim 52)$ |
| Hw | 3.33 | 4.27 | 6.41 | $0.4425e^{0.0523x}$ | 38.59 | 43.34 | 51.11 |
| Hl | 2.29 | 2.39 | 3.97 | $0.3350e^{0.0462x}$ | 41.60 | 42.53 | 53.51 |
| $P_1f$ | 2.29 | 2.92 | 4.49 | $0.2657e^{0.0528x}$ | 40.79 | 45.40 | 53.55 |
| $P_1$tib | 2.08 | 3.13 | 4.23 | $0.2912e^{0.0510x}$ | 38.55 | 46.56 | 52.47 |
| $P_1$tar | 1.46 | 1.7 | 2.43 | $0.1940e^{0.0474x}$ | 45.79 | 45.79 | 53.33 |
| $P_2f$ | 3.13 | 4 | 5.51 | $0.3116e^{0.0548x}$ | 42.10 | 46.58 | 52.42 |
| $P_2$tib | 2.5 | 3.65 | 5.22 | $0.3235e^{0.0527x}$ | 38.80 | 45.98 | 52.77 |
| $P_2$tar | 1.58 | 1.78 | 2.95 | $0.2030e^{0.0472x}$ | 43.47 | 46.00 | 56.70 |
| $P_3f$ | 3.75 | 4.27 | 6.02 | $0.3659e^{0.0574x}$ | 40.54 | 42.81 | 48.79 |
| $P_3$tib | 2.81 | 3.84 | 5.77 | $0.3654e^{0.0532x}$ | 38.34 | 44.21 | 51.87 |
| $P_3$tar | 1.56 | 2.08 | 3.85 | $0.2324e^{0.0445x}$ | 42.79 | 49.25 | 63.09 |
| Thl | 1.98 | 3.23 | 3.21 | $0.3073e^{0.0504x}$ | 36.96 | 46.67 | 46.55 |
| Thw | 2.4 | 3.65 | 3.97 | $0.3174e^{0.0546x}$ | 37.05 | 44.73 | 46.27 |
| Al | 6.56 | 8.75 | 14.1 | $0.8517e^{0.0542x}$ | 37.67 | 42.98 | 51.78 |
| Aw | 3.13 | 5.31 | 7.44 | $0.5095e^{0.0546x}$ | 33.25 | 42.93 | 49.11 |

| feature | y = | $R^2$ | feature | y = | $R^2$ |
|---|---|---|---|---|---|
| Hw | $0.3022e^{0.2673x}$ | 0.9168 | $P_3f$ | $0.2433e^{0.2913x}$ | 0.9598 |
| Hl | $0.2388e^{0.2364x}$ | 0.9490 | $P_3$tib | $0.02505e^{0.27x}$ | 0.9532 |
| $P_1f$ | $0.1842e^{0.2665x}$ | 0.9259 | $P_3$tar | $0.1708e^{0.2257x}$ | 0.9507 |
| $P_1$tib | $0.2053e^{2566x}$ | 0.9628 | Thl | $0.2197e^{0.2521x}$ | 0.9914 |
| $P_1$tar | $0.1409e^{0.2392x}$ | 0.9748 | Thw | $0.2162e^{0.2765x}$ | 0.9587 |
| $P_2f$ | $0.2102e^{0.2787x}$ | 0.9393 | Al | $0.5861e^{0.2733x}$ | 0.9782 |
| $P_2$tib | $0.2228e^{0.2673x}$ | 0.9467 | Aw | $0.3417e^{0.279x}$ | 0.9195 |
| $P_2$tar | $0.1466e^{0.238x}$ | 0.9714 | | | |

## Observations

The larva was first noted by chance on day seven of the incubation of the mud. It may, of course, have become active earlier. It hid by day in the vegetation of the aquarium, and hunted at night. However, it was not before the 9th instar (see hereafter) that an exuvia could be recovered. In all, only three larval exuviae were collected, as it was difficult to locate them. The three exuviae were collected 31, 36 and 52 days after first incubation.

The fifteen measurements of the three exuviae (see Table 3), each fitted to an exponential growth rate, were converted into larval ages (Table 3). They were identified as 9th, 10th and 12th instar. This was corroborated by using qualitative features from Lamb (1923, 1925) and Kumar (1984), such as the number of premental setae, length of the wing cases, and by the fact that the 12th instar was followed by emergence.

Calculations of the age of each of these instars (as the arithmetic mean of fifteen separate estimates) gave 40, 45 and 52 days, respectively (Table 3). Using data by Kumar (1984), we find a slight difference: 38, 42 and 58 days, respectively (see Table 2), excluding the egg stage. Kumar (1984) reared his animals at a temperature of 28-32 °C, while the Brazilian larva was kept under a constant temperature of 30 °C (±1 °C). Larval development in Odonata shortens at higher temperatures (Mathavan, 1990), but the temperature regimes are sufficiently close to make the respective data sets comparable. The agreement for stages 9 and 10 is good, but for stage 12, Kumar's estimate of total development time is 6 to 7 days longer. Thus, the larva may have been 52, but also 59 days old when it emerged.

## Discussion

Was the larva observed in our aquarium an egg or a dormant larva at the time of collection? Warren (1915) found a minimum time of 55 days for Hawaiian *Pantala flavescens* larvae to reach maturity. Lamb (1923) cites an average of 80 days, varying from 65 to 101 days. Kumar (1984) records experimental durations from 56 to 61 days. If our mud sample had contained an egg of *Pantala flavescens* and if this had hatched on the first day of incubation, larval life would have been completed in 52 days. This is at least three days shorter than Warren's estimate, which seems improbable. Hatching of the egg on the first day of wetting, though not theoretically excluded, is unlikely, because the egg would first need a period of rehydration. Moreover, a larva hatching too soon after wetting might find nothing to eat in its environment.

More likely, the *Pantala* was already a larva when transported to Europe. Compared with the mean ages for the 9th, 10th and 12th instar found by Kumar (table 4), it was probably 6-7 days old when it resumed activity. If so, it was a larva of the 2nd-4th instar (see 'note').

As the freshwater pools in the Lençóis Maranhenses were already dried out long before my collection, December being the last month of the dry season, a larval *Pantala* would have been in dormancy or quiescence for at least a few months. It did not occur in a humid micro-environment, and it was not collected by digging, under a rock, or in the cracks of a tree trunk. It clearly was present in sand, between dry crusts of filamentous algae, among detritus, or inside an empty *Ampullaria* shell.

The rapid larval development of *Pantala flavescens* has been widely cited as a strategy to successfully colonise temporary waters (see Hodgkin & Watson, 1958). It seems to be tacitly understood that oviposition and larval development take place while these biotopes are inundated, and that development from egg to imago takes place uninterruptedly. However, it is clear that a capacity for interrupting larval development by going dormant in a dry state, to resume activity at the next inundation, would be a powerful adaptation to aridity and the ensuing unpredictability of its aquatic environment.

The few records of drought resistance in dragonfly larvae common in arid and dry climates, and reproducing in ephemeral ponds were first discussed by Corbet (1962), who expressed astonishment at the scarcity of data available. Strangely, in *Pantala flavescens*, one of the most widespread libellulids on earth, larval drought-resistance has never been reported. However, one of the main reasons for this may simply be that dried-out freshwater pools are and hardly ever sampled for dragonfly larvae. Our discovery was unintentional.

Drought resistance in odonate larvae may might be more widespread than hitherto believed. The old experiments of Tillyard (1910), subjecting larvae of *Synthemis eustalacta* (Burmeiser, 1839) to periods of drought of up to ten weeks, have long been regarded as a curiosity. But Willey & Eiler (1972) found that larvae of *Somatochlora semicircularis* Delys, 1871 - adapted to live in summer-dry high-altitude ponds - are capable of digging in sand, under rocks, and thus survive in what might at least be a semi-dry state. Dumont (1979), digging in the bottom of a dried-out freshwater pool in the Tassili-n-Ajjer, Central Sahara, stumbled upon an aggregation of larvae of *Trithemis arteriosa* (Burmeister, 1839) and *Orthetrum chrysostigma* (Burmeister, 1839) at a depth where the sand was becoming damp. All these fortuitous observations at least suggest that the phenomenon of drought-dormancy in dragonfly larvae merits a systematic investigation. For example, Hawking & Ingram (1994) note that, in the mediterranean-subtropical climate of South Australia, larvae of *Pantala flavescens* emerge about 51 days after ponds get inundated. They conclude therefore that oviposition (by strays arriving from the north), and egg and larval development all took place within that span of time. Here, we suggest that dormant larvae may have been present in the bed of the ponds studied, and that they resumed their development as soon as the ponds contained free water.

**Note**

During an expedition to the island of Socotra (Yemen) in February 1999, the first author took the opportunity of testing the possibility of drought resistance in two fully grown *Pantala flavescens* larvae. They were air-dried and kept separately in small containers. Both animals did not survive for more than 24 hours. This observation raises the possibility that the larvae of *Pantala flavescens* might lose their ability to survive drought when older than a certain instar.

## Acknowledgements

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