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International Journal of Odonatology

Publication details, including instructions for authors and subscription information:

<http://www.tandfonline.com/loi/tijo20>

Ovo-viviparity in the Odonata? The case of *Heliocypha perforata* (Zygoptera: Chlorocyphidae)

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Published online: 09 Dec 2014.

To cite this article: H. G. Salindra K. Dayananda & Roger L. Kitching (2014) Ovo-viviparity in the Odonata? The case of *Heliocypha perforata* (Zygoptera: Chlorocyphidae), International Journal of Odonatology, 17:4, 181-185, DOI: [10.1080/13887890.2014.959076](https://doi.org/10.1080/13887890.2014.959076)

To link to this article: <http://dx.doi.org/10.1080/13887890.2014.959076>

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Ovo-viviparity in the Odonata? The case of *Heliocypha perforata* (Zygoptera: Chlorocyphidae)

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(Received 14 May 2014; accepted 25 August 2014)

In this paper we record a likely instance of ovo-viviparity in a chlorocyphid damselfly from south-western China. If confirmed, this will be the first record of live birthing in the Odonata: indeed in any member of the Palaeoptera. The widespread Asian damselfly *Heliocypha perforata* (Percheron, 1835) is proposed to be, at least facultatively, viviparous. A female was observed and filmed appearing to deposit pro-larvae directly onto the exposed surface of a half-submerged branch in a small stream in Xishuangbanna Autonomous Dai Prefecture, Yunnan, China. The species is known to deposit eggs in bark crevices close to water but no previous case of actual live births is known.

Keywords: Odonata; dragonfly; damselfly; ovo-viviparity; Yunnan; Chlorocyphidae

Introduction

The vast majority of insects, including all odonates investigated to date, are oviparous (Corbet, 1999; Grimaldi & Engel, 2005; Gullan & Cranston, 2010): that is, they reproduce by producing eggs which develop and hatch at some later time. A few, often highly specialized insects are live-bearing (see below and Supplementary Material). In this paper we record the phenomenon in the Odonata for the first time.

Live bearing in insects occurs when eggs or larvae are retained within the uterus either being nurtured as embryos by various means within the body of the female parent ('viviparity' *sensu stricto*), or hatching immediately upon being laid ('ovo-viviparity'). True viviparity may take one of three forms (Gullan & Cranston, 2010). Unlaid eggs may be nurtured through a placenta-like structure (e.g. in aphids, some Dermaptera, some Psocoptera and polyctenid bugs). Alternatively, eggs may hatch internally and pre-birth larvae feed on glandular structures within the female reproductive tract (e.g. in the Diptera: Hippoboscoidea). Finally, in the Strepsiptera and the Diptera: Cecidomyiidae, larvae hatch into the haemolymph of the parents and are nurtured there, emerging as fully formed larvae. In the case of the Cecidomyiidae these larvae consume the female during development (Gagné, 1981; Schüpbach & Camenzind, 1983). Ovo-viviparity, in contrast, occurs where 'normal' eggs are retained inside the female and eclose either immediately

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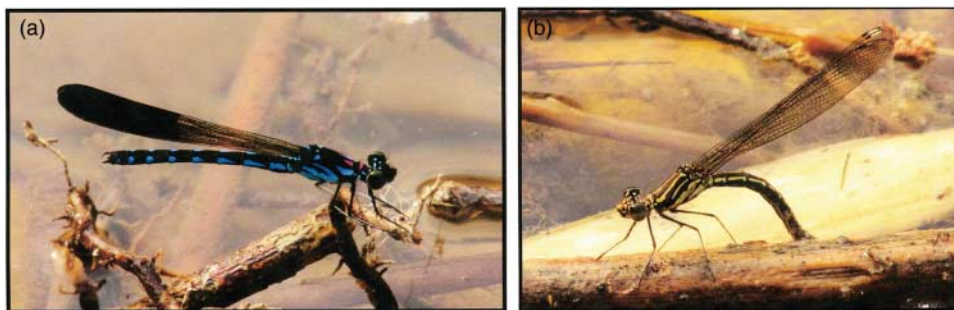


Figure 1. *Heliocypha perforata* (a) male, (b) female.

upon or just before oviposition. Isolated examples of this habit occur within several orders including the Coleoptera, Diptera and Thysanoptera.

The Odonata are typically oviparous and, in the Zygoptera, eggs are inserted into a substrate, typically plant matter, at or close to the surface of the larval habitat. An incubation period varying from days to weeks follows (Stoks & Córdoba-Aguilar, 2012). The semi-mobile pro-larva emerges from the egg either directly into the aquatic environment or rapidly makes its way into fresh water from the oviposition site. Once in the water it ecdyses into the second instar larva almost immediately.

Heliocypha perforata limbata (Selys, 1879) (Figure 1a, b) is a medium-sized, widespread species of the family Chlorocyphidae, found throughout mainland south-east Asia and north-east India reaching the subtropical and tropical regions of China. Eggs are normally inserted into large intact pieces of dead wood at the waterline beside swift flowing water within a male's territory. Group oviposition is common (A. G. Orr, pers. comm.).

Observations

The observations of *H. perforata* were made by SKD during a natural history excursion to the banks of the Ruosuo river, a large tributary of the upper Mekong in Yunnan, China (21°55'74.78" N, 101°19'20.54" E, elevation 559 ± 5 m). The river is slow moving and shallow, about 40 m wide at the point in question with alluvial banks. The area is surrounded by a typical subtropical Chinese landscape with a combination of remnants of natural vegetation, rubber plantations and market gardens (Cao, Zou, Warren, & Zhu, 2006). The river banks have muddy access points, and banks of shrubs or grass. Individuals of both *H. perforata* and *Neurobasis chinensis* L. were observed flying together at the site. Both male and female *H. perforata* were part of the population.

A female individual was observed and subsequently filmed while appearing to search for an oviposition site on an emergent log. Before filming began SKD observed the female and a recently laid prolarva on the surface of the log. In response, filming began. The female appeared to be probing the crevices on the log with its abdomen as if seeking an oviposition site. Dipping her abdomen in the water the female then appeared to scribe a line of moisture from the water surface onto the log to the point at which she, in all probability, produced a second prolarva. Here, as is clear on the video, her abdomen tip encountered a small fragment of debris. The prolarva was seen clearly by SKD and judged to emerge from her abdomen tip. The newly laid prolarva became entangled with the debris scrap but is clearly seen to leave it behind as it heads for the water surface. Figure 2a, b has been traced from the video and represents the sequence of events

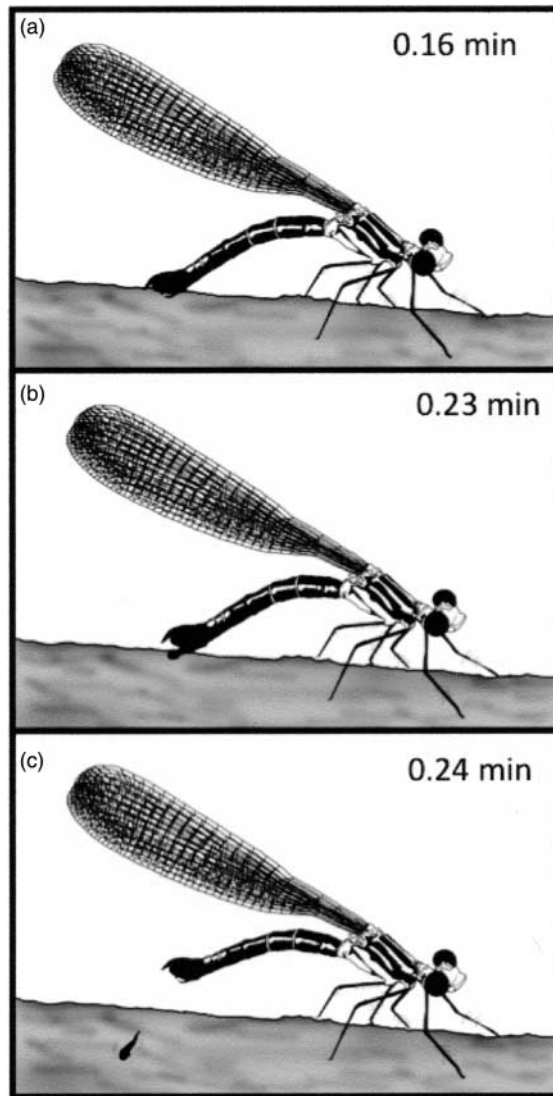


Figure 2. Schematics of a time sequence of apparent ovo-viviparity in a *Heliocypha perforata* female in Yunnan Province, south-western China. These are sketches based on the video recording which is available in the Supplementary Material.

surrounding observation of the second parturition event (the first to be actually videoed). Sixteen seconds after the observations began (that is, 29 s into the entitled and edited video) the female touched her abdomen tip on the surface of the log (Figure 2a). Seven seconds later a prolarva appeared to emerge from between the gonopophyses of the female's abdomen tip (Figure 2b). This presumed parturition event was completed in less than 2 s and the active prolarva wriggled down to the water surface in the water film that coated the log (indicated schematically in Figure 2c). An edited version of the video clip is available in the Supplementary Material. Apart from the main observation, SKD observed one male very near to the female subject and three males were also observed roughly 5 m away from the female subject; but there were no other females.

Discussion

A remarkable and unique observation of this kind raises many questions that only much more intensive follow-up work can attempt to answer. Two of these questions are of particular importance.

Perhaps the central question concerns the nature of the observed viviparity and how it fits within the typology described in the earlier brief review of live birthing in the Insecta. All three categories of true viviparity seem unlikely in this case. All require special structural adaptations which are simply absent in odonates. Even pseudo-uterine viviparity, the most widespread of the described forms, requires a placenta-like structure to nurture the retained eggs. This adaptation has emerged at least four times within the neopterous Hemimetabola but in three of these cases is associated either with a colonial parthenogenetic habit (the aphids, see Kennedy & Stroyan, 1988) or with specialized ectoparasitism (the polyctenid bugs, see Hagan, 1931; and, the hemimerine and arexinine Dermaptera, see Tworzydło, Kisiel, & Blinski, 2013). The other two forms of true viviparity are taxonomically highly derived (in the Hippoboscoidea, Strepsiptera and Cecidomyiidae) and simply implausible within the Odonata. Dismissing these more specialized mechanisms points clearly to this being a form of ovo-viviparity even though there is no trace of the egg membrane in the video.

Given that, in the Odonata, fertilization is generally supposed to occur just before oviposition as the eggs pass the bursa copulatrix (Corbet, 1999; Córdoba-Aguilar, Uhía, & Cordero Rivera, 2003), then, this suggests one of two explanations. Either fertilization occurred and the eggs were then retained within the female reproductive system where they matured and hatched just before the observed parturition event, or this was a case of parthenogenesis.

Both options would represent notable aspects of the species' biology. Eggs would have had to spend an extended time within the oviducts comparable to the usual incubation time (Stoks & Córdoba-Aguilar, 2012) that occurs following normal oviparous reproduction. If these are parthenogenetic offspring then the species joins the exclusive company of the Azorean populations of *Ischnura hastata* (Coenagrionidae) (see e.g. Lorenzo-Caballa & Cordero-Riviera, 2009). In this species diploid offspring are produced by thelytoky exclusively from female genetic material: offspring accordingly are also uniformly female. This mechanism is unlikely in *H. perforata* first because males were present and, second, because females may well have needed access to a male's territory before any offspring production became possible.

A second key question relates to the extent of this form of reproductive behavior at the level of the species, population and/or individual. In a similarly sized chlorocyphid zygopteran, *Libellago semiopaca* (Say), in Borneo, lifetime production of a female was estimated at 600 eggs with each requiring up to five minutes for oviposition (Orr, 2009). If Orr's (2009) observations were to be applicable to *H. perforata*, then viviparity of the kind described here would reduce lifetime fecundity substantially. Crespi (1989) speaks of *facultative* viviparity in a species of Thysanoptera. Females of *Elaphrothrips tuberculatus* can apparently switch between viviparity and oviparity, producing only males by the former mechanism and females by the latter. Viviparously produced offspring are fewer but with higher survivorship after birth. If we assume that oviparity is the norm in *H. perforata* then a facultative switching of the sort recorded by Crespi (1989) could be an explanation for our current observations, perhaps in response to a shortage of suitable oviposition sites and/or repeated harassment by males.

So we are left with three complimentary hypotheses. First that viviparity in this species is a simple case of ovo-viviparity with fertilized eggs retained while they mature. Second, that in fact this represents an additional example of parthenogenesis within the order and no fertilization process is involved. Third, this behavior (whatever its exact nature) may be intermittent and facultative in response to unknown environmental cues. Resolution of these questions awaits further observations. It will be pertinent to examine the genital anatomy of the species as well

as making further observations of individuals within the population. Ultimately comparisons of genotypes of females and offspring would resolve the second question. Detailed population ecological investigation may resolve the third hypothesis. All of these await further research.

In conclusion, we stress that this remarkable observation was of one female on one occasion. We suggest that the most parsimonious interpretation of the observation is that this was a case of ovo-viviparity. Other explanations are possible. Potentially a pre-existing prolarva could have become engaged with the tip of the female's abdomen. Alternatively the female could have been returning to a previous oviposition site to 'assist' the prolarva in eclosing. Other, more or less unlikely, explanations may exist and we stress that the nature of the observation demands confirmation. If this is indeed a case of ovo-viviparity then the question of how common is the phenomenon remains a matter for speculation.

Acknowledgements

SKD thanks Rachakonda Sreekar, Mareike Roeder and Lu Yun for assistance in the field, Christos Mammides and Eben Goodale for encouraging publishing of this observation and the Chinese Academy of Sciences, for the studentship during which these observations were made. RLK thanks the Chinese Academy of Sciences for their provision of a Senior Visiting Professorship held at XTBG. Both authors thank Pierre Honoré for editing the video, and we are grateful to a number of senior odonatologists who freely provided advice during the preparation of this account including reviewing and improving an early version of the manuscript. These were Dr Albert Orr (Brisbane), Dr Robby Stoks (Leuven), Dr Frank Suhling (Braunschweig) and Dr Andreas Martens (Karlsruhe). We acknowledge and appreciate the financial support of the 1000 Plan Recruitment Program of Global Experts of the People's Republic of China to Eben Goodale.

Supplemental data

Supplemental data for this article can be accessed via the online version [<http://dx.doi.org/10.1080/13887890.2014.959076>].

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