PAEDOGENESIS IN *ERISTALIS ARBUSTORUM* (DIPTERA: SYRPHIDAE)

Bart Achterkamp*, Mart Ottenheim[#], Leo Beukeboom[#] & Paul Brakefield*

Institute of Evolutionary and Ecological Sciences,
Section of Evolutionary Biology* & Section of Animal Ecology[#],
Leiden University, P.O. Box 9516, 2300 RA Leiden, The Netherlands.

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Summary
Paedogenesis is the reproduction of larvae or juveniles. In insects this form of reproduction is known from one beetle, several species of gall midges and possibly *Eristalis tenax*. This study aims to show paedogenesis for *E. arbustorum* under laboratory conditions. In total 1266 larvae were reared in individual containers and five occasions of paedogenesis were recorded among 560 successful pupations. In all cases one larva was put in the container and two larvae or pupae were collected later. The life history consequences of this way of reproduction are discussed.

INTRODUCTION

Animals vary widely in the timing of reproduction. In many insects for example, the reproductive organs take days to mature, whereas in others copulation and oviposition occur almost immediately after the last moult. Some species take this trend even further and reproduce before the adult stage; this is called *paedogenesis*. Reproduction by budding or fission in juveniles occurs in some groups of animals (Craig *et al.*, 1997). In insects however, the reproduction starts with cells from the germ-line. Only primary reproductive organs (i.e. ovaries) need be present. Therefore, in most cases there is no copulation and no fertilisation and the reproduction involves parthenogenesis i.e. 'An egg cell developing into a new individual without fertilization.' (Von Siebold, 1856; Suomalainen *et al.*, 1987). Parthenogenesis is, however, not necessary for paedogenesis, as is evident in the bat-bug *Hesperoctenes fumarius* (Hagan, 1931).

Much confusion exists about the definitions of paedogenesis and the related terms polyembryony, progenesis and neoteny. Polyembryony is the splitting of one embryo into many before the end of embryogenesis (Hardy, 1995). In humans, polyembryony may result in identical twins, and can be regarded as a 'mistake', but in some insect species polyembryony has been developed into an alternative mode of reproduction as, for example, in the parasitoid wasp *Copidosoma floridanum* (Strand and Grbic, 1997). The female lays a single egg in the egg of the host insect. While the host larva grows, the single parasitoid embryo develops into 1500-2000 morulae that subsequently follow the normal development to the larval stage.

The maturation of gametes before the completion of body growth is termed progenesis (Giard, 1887 in Gould, 1977, p 226). In insects, copulation occurring almost immediately after the last moult is a regular phenomenon. It is therefore not surprising that mature eggs and sperm can be found in juvenile individuals. Generally fertilisation cannot take place in juveniles and reproduction is restricted to adults. Only in parthenogenetic animals is the phenomenon functionally interesting: for example, almost all aphids (Heteroptera: Aphididae) show progenesis (Suomalainen *et al.*, 1987). Embryos start development long before their mother reaches adulthood. In aphids, young are only incidentally born before the mother is an adult and hence paedogenesis is rare (Wanjama and Holliday, 1987). The progenesis in the rare bat-bug *Hesperoctenes fumarius* (Heteroptera: Polyctenidae) is similar, but here a peculiar, haemocoelic insemination occurs and the reproduction is sexual. Although juveniles can carry big

offspring, paedogenesis resulting from this case of progenesis has not yet been observed (Hagan, 1931). Would a juvenile in this species be observed to give birth, then this would represent the first case of bisexual paedogenesis in insects.

Sometimes adults show one or more juvenile features. This situation is defined as neoteny (Giard 1887 in Gould, 1977). The adult and juvenile features can be inferred from individuals of the same species that show normal development, or from a comparison with related (even ancestral) species. The distinction with paedogenesis and progenesis is in the underlying mechanism rather than in the result. Neoteny arises when physical maturity is retarded, whereas progenesis results from an acceleration in sexual maturation (Gould, 1977).

Paedogenesis in insects

The most interesting cases of paedogenesis can be found in three holometabolous groups: several gall midges (Diptera: Cecidomyiidae), the beetle *Micromalthus debilis* (Coleoptera, Archostemata: Micromalthidae), and possibly the hoverfly *Eristalis tenax* (Diptera: Syrphidae).

Paedogenesis occurs in at least seventeen species of gall midges (Diptera: Cecidomyiidae) (Wyatt, 1967; Mamaev and Krivosheina, 1993). The species that has been best studied is *Heteropeza pygmaea* Winnertz. After mating the adult *H. pygmaea* female lays a very small (1-2) number of large eggs. From the eggs, female larvae hatch that feed on fungal mycelia. Very soon, eggs start to develop in their ovaries from germ line cells and are released in the haemocoel. Growth of this mother larva, oocyte growth and embryogenesis occur at the same time and within a week the mother larva moults into a "hemipupa" hidden under the larval cuticle and her body is completely histolysed. The embryos have then matured into larvae and subsequently hatch from the dead mother to start a paedogenetic life of their own. Under suitable nutritional conditions, paedogenetic reproduction can go on for at least 250 generations (Ulrich, 1936). Under certain conditions new-born larvae follow a different development, leading to pupae and adults of both sexes. Kahle, 1908; Ulrich, 1936; Wyatt, 1963; Suomalainen, 1987).

Micromalthus debilis, the only known beetle with paedogenesis, occurs in eastern North America and has been introduced to South Africa. The larvae live in and feed on rotten wood. The life cycle is complex and not entirely known. The paedogenetic, thelytokous female larva produces eggs, which mature into embryos and larvae inside her body. After the third larval instar the all-female offspring can basically follow three developmental pathways: they can pupate and become an adult female, they can moult into the paedogenetic "larva" or they can moult into a male-producing larva.

The male-producing larva produces one big egg, which adheres to its body. From this egg, a male larva hatches, which eats his mother instead of wood. When she is completely eaten the male pupates and emerges as an adult. If the egg fails to develop, the male-producing larva produces a small number of female thelytokous larvae (Barber, 1913; Scott, 1938; Pringle, 1938).

Paedogenesis has been reported and photographed in *Eristalis tenax* (Ibrahim & Gad, 1975). Supernumerary larvae were incidentally observed by Ottenheim (unpublished data) in *E. arbustorum*. The purpose of the present study was to demonstrate paedogenesis in *E. arbustorum* under controlled laboratory conditions.

MATERIAL AND METHODS

Gravid females were collected in and around Leiden (The Netherlands) in summer 1999. These flies were kept in gauze cages with a honey-pollen solution and flowers, mainly *Senecio jacobaea*. A tray was placed in the cages with rotting flower stems and some water. Females tended to land on the flower stems and laid up to 150 eggs just above the water surface.

New egg batches were collected daily and placed on fresh water. After hatching, the larvae were transferred in batches of 50 larvae to trays with water and rotting plant cuttings of *S. jacobaea*. In previous experiments, this environment seemed to have induced paedogenesis in *E. arbustorum* (Ottenheim, personal observation). After a short period, usually of three days, larvae were transferred to individual containers with the optimal rearing medium of rabbit dropping soup with yeast, according to Ottenheim *et al.* (1995). To check that no *Eristalis* larvae or eggs where already present in droppings from the dry coastal dunes, 10 control trays with each 500ml medium were set up. No larvae ever developed in these controls. The individual containers consisted of a small plastic tray filled with approximately 20ml of medium, inside a larger transparent tray of 250ml, which was closed with a lid. Very small holes were made in the lid to allow airflow.

To ensure that only one larva was transferred to an individual container, a larva was transferred to a petri dish with fresh clear water, where a check was made that it was really one. This procedure was repeated with a second dish with fresh water, before the single larva was transferred to the individual container. The experiment was performed at 20°C and a 16:8 L:D light regime. The containers were checked for pupae every two days from day sixteen to day twenty-four after hatching. The containers were thoroughly checked for any living or dead larvae before they were disposed of.

RESULTS

1266 larvae of 16 families were used in this experiment. Successful pupation occurred in 45% of the larvae, resulting in 560 pupae, some additional larvae went into diapause. Five occurrences of paedogenesis were found. The circumstances under which they occurred are summarized in table 1. Larval development time was on average 27 days. No exact estimate of development time could be made. The development times of the paedogenetic larvae are shown in table 1 and fall well within the normal range of larval development time, see figure 1. Here the duration between the start of individual development in dropping soup and pupation are depicted, with arrows for the six known paedogenetic development times. In the last category, also individuals in diapause at the end of the experiment are counted.

Table 1. Summary of recorded paedogenesis.

Batch and individual number	Number of days in *Senecio*	Transfer date	End date	End phase	Larval development time (days)
Mc 50	3	18-aug.	4-sept.	Pupa	20
			4-sept.	Pupa	20
Mc 68	3	18-aug.	8-sept.	Pupa	24
			4-oct.	Dead big larva	-
Md 38	3	18-aug.	31-aug.	Dead small larva	-
			4-oct.	Dead big larva	-
Rg 8	19	10-sept.	21-sept.	Pupa	30
			24-sept.	Pupa	33
Me 112	22	9-sept.	21-sept.	Pupa	34
			5-oct.	Diapausing larva	>48
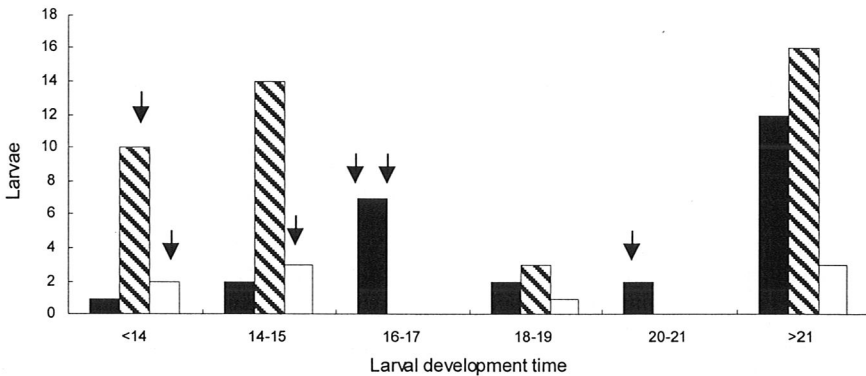
Figure 1. Recorded larval development time in the good medium. The arrows indicate the cases of paedogenesis in the different egg batches. Solid bars are Mc, striped bars are Me, and open bars are Rg.

DISCUSSION

This study shows that *E. arbustorum* larvae are able to reproduce and therefore document paedogenesis in *Eristalis*. Up to now we only found a doubling of the larvae but Ibrahim and Gad (1975) found two cases of three offspring from single *E. tenax* larvae. Larval development was not slowed down, which together with the finding of a small larva in container Md 38, could mean that the reproduction took place in an early stage. For example, paedogenesis might have happened immediately after the transfer from the *Senecio* to the optimal medium. The paedogenetic *E. tenax* larvae were final instar (Ibrahim & Gad, 1975).

Under our study conditions, paedogenesis in *E. arbustorum* does not seem to occur often, as we found it only in 1 % of the larvae. We tried to induce paedogenesis by the bad/good medium switch treatment but this did not seem to work very well. A possibility is that the containers are too small and paedogenesis would almost immediately result in overcrowding. Ottenheim (unpublished data) also observed paedogenesis in only rabbit dropping soup with yeast, the good medium. In these occasions 20 larvae were put in a tray of 200ml from which 28 and 23 larvae pupated. This suggests that larval interactions may induce paedogenesis.

The developmental mechanism of the paedogenesis is not known but it is likely to start from the ovaries, as it does in all known paedogenetic insects. This would also mean that males are not able to engage in paedogenesis and all resulting adults would be females. Adult *Eristalis* females take days to mature their eggs, and the acceleration in ovarian development needed in paedogenesis is remarkable. The mode of parthenogenesis is unknown, so it is not possible to state whether the two larvae found per container are clones or that recombination somehow has taken place.

The importance of paedogenesis in the life history of *E. arbustorum* is not clear. We suggest that paedogenesis is advantageous under the following conditions: 1) when climatic conditions are such that adults cannot function but larvae can, for example during diapause from September to March; and/or 2) when very suitable but ephemeral habitats are encountered, e.g. cattle dung, large amounts of grass cutting or dead animals rotting in water. The advantage depends on mortality and fecundity in the different stages in the field, but these data are lacking. It can also be argued that paedogenesis in *Eristalis*

arbustorum is not adaptive but a rare accident, perhaps comparable to identical twins in humans.

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