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Title: The uniqueness of spider lactation in arthropods

Authors: Bing Dong^{1,2}, Tristan Charles-Dominique³, Richard T.

Corlett⁴, Rui-Chang Quan⁴, Zhanqi Chen^{1,2*}

Authors' affiliations:

¹Key Laboratory of Tropical Forest Ecology, Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences, Yunnan 666303, China

²Center for Plant Ecology, Core Botanical Gardens, Chinese Academy of Sciences, Yunnan 666303, China

³CNRS UMR7618; Sorbonne University; Institute of Ecology and Environmental Sciences Paris; 4, place Jussieu, 75005 PARIS

⁴Center for Integrative Conservation, Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences, Yunnan, 666303, China.

***To whom correspondence should be addressed.**

E-mail: chenzhanqi@xtbg.ac.cn

We published a report showing that female jumping spiders from the species *Toxews magnus* provide nutritious milk from their epigastric furrow to their offspring, and further, that this milk provisioning is accompanied by extended parental care until the subadult stage (1). We suggested that this method of food provisioning in *T. magnus* is the closest analogue to mammalian milk provisioning ever described for a non-mammal. In a response to our report, Benoit et al. (2) argued that while our description is another interesting example of food provisioning in arthropods, many other non-mammals provide similar milk-like substances to nourish their offspring, and they provided several arthropod examples. We reaffirm here our claim that the milk-provisioning described in *T. magnus* contrasts with other known examples of non-mammal food provisioning (including all those mentioned by Benoit et al.), based on five important factors which make it comparable to mammalian lactation. The criteria used to separate the feeding types (Table 1) are: 1) whether the food is secreted by the mother (as opposed to regurgitation of food she consumes); 2) whether the food is supplied after birth/hatching (as opposed to prenatal/pre-hatching nutrient supply) ; 3) whether the food is provided continuously to juveniles (as opposed to a one-off provisioning of food at the egg stage); 4) whether the juvenile depends on the mother for their nutrition or can survive independently; 5) whether mother and juveniles interact behaviorally with each other for milk feeding. Based on these factors, food provisioning can be classified into six distinct types (Table1), which are all currently widely recognized as separate phenomena involving contrasting physiological and behavioural traits: insect viviparity, prey regurgitation,

mass provisioning, embryo nourishment, matrophagy, trophic eggs and lactation, with the last of these so far only found in jumping spiders and mammals.

We agree with Benoit *et al.* that there are other examples of arthropods providing nutritive fluids to their offspring and acknowledged this point in our initial report.

However, within the word limit we could not expand on the differences between milk provisioning in jumping spiders and food provisioning in other arthropods. To address the query from Benoit *et al.*, we here provide more details on the different types of food provisioning observed in arthropods and how they differ from what we reported for *Toxeus magna*. Among the organisms cited by Benoit *et al.* as providing ‘milk-like substances’:

- **Tsetse flies** (*Glossina morsitans*) and **cockroaches** (*Diploptera punctate*) provide nutritive fluids at a prenatal phase, either for intrauterine larvae (3) or for developing embryos in the brood sac (4, 5, 6). This type of food provisioning, which can be labelled insect viviparity, does not require any behavioural interaction between mother and offspring. In contrast with lactation in *T. magna*, in which mother-offspring interactions last from parturition to weaning, it is therefore not expected to be associated with advanced social interactions such as learning.
- **European earwig** (*Forficula auricularia*) and **burying beetle** (*Nicrophorus vespilloides*) females regurgitate food to their nymphs (7, 8, 9). Unlike lactation, this type of feeding does not require a secretory organ and is likely to be less costly to the mother than synthesizing milk. Feeding by

regurgitation and milk provisioning are usually considered to be distinct types of parental food provisioning (8).

- **Some non-social wasps, ants, all the eusocial vespoid wasps**

(Stenogastrinae, Polistinae and Vespinae) **and most eusocial bees**

(subfamilies: Allodapinae, Bombinae and Apinae) also supply food for their

nymphs (10, 11, 12). For non-social species, this feeding is done through

mass-provisioning where, in contrast to lactation, each egg is sealed into a cell

containing all the food required for development, and the offspring is

nutritionally independent of its mother 1-2 days after oviposition. Further, the

food provisioning is done by prey capture by sibling offspring, not by

maternal secretion. For eusocial species, such as honeybees (Apinae), paper

wasps (Polistinae), and ants, food may be provided continuously for an

extended period, but this differs from lactation in that the food is not processed

by the mother, but simply regurgitated, and there is no interaction between

mother and offspring, as the food is provided by colony co-workers (older

siblings) (10). As we discussed in our original paper, the most similar type of

feeding to that described for *T. magnus* is found in arthropods providing

trophic eggs as food (13), with the important difference that there are no

parent-offspring interactions involved.

To conclude, we believe that the phenomenon described in our report is novel in non-

mammals, differs in important ways from other examples of arthropod food

provisioning, and is most similar to mammalian milk-provisioning. There are, of

course, also commonalities between modalities of parental food provisioning (Table 1) that can be used to address important questions related to the evolutionary and ecological consequences of food provisioning in the Arthropoda.

Lastly, we also agree with Benoit *et al.* that the evolution of parental care is classically hypothesized as being a response to harsh environments and predation, and that E. O. Wilson's work decades ago was prominent in establishing these hypotheses. However, we suggest here that these explanations probably extend to lactation and extended parental care in arthropods; both phenomena new to Science described in our report. Long-lasting maternal care, with the mother caring for sexually mature offspring, has only been described for arthropods in *T. magnus* (1). It was previously assumed to have evolved only in some long-lived social vertebrates, such as primates, while it is absent in most mammals, such as the Guinea pig (*Cavia porcellus*) (8, 14).

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Table legend:

Table1: Comparisons of parental food provisioning and parental care among species of Mammalia, Arachnida, and Insecta. The colors indicate consistence, green: yes; red: no.

Species	Form	Food provisioning					Parental care		Reference	
		Maternal secretion	After birth/hatch	Continuous	Required	Mother-offspring interaction	After nutritional independence	After sexual maturity		
MAMMALIA	Human	<i>Homo sapiens</i>	Lactation	■	■	■	■	■	■	(8)
	Guinea pig	<i>Cavia porcellus</i>	Lactation	■	■	■	■	■	■	(14)
ARACHNIDA	Spiders	<i>Toxews magnus</i>	Spider milk	■	■	■	■	■	■	(1)
		<i>Amaurobius ferox</i>	Trophic eggs	■	■	■	■	■	■	(13)
	Pseudoscorpions	<i>Paratemnus elongatus</i>	Embryo nourishment	■	■	■	■	■	■	(5)
		<i>Paratemnoides nidificator</i>	Matriphagy	■	■	■	■	■	■	(6)
INSECTA	Tsetse fly	<i>Glossina morsitans</i>	Viviparity	■	■	■	■	■	■	(2,3)
	Cockroach	<i>Diploptera punctata</i>	Viviparity	■	■	■	■	■	■	(4)
	Earwig	<i>Forficula auricularia</i>	Regurgitation	■	■	■	■	■	■	(7)
	Burrying beetle	<i>Nicrophorus vespilloides</i>	Regurgitation	■	■	■	■	■	■	(9)
	Solitary wasp	<i>Trypoxylon politum</i>	Mass provisioning	■	■	■	■	■	■	(11,12)