



# Letter to the editor referencing “The apparent kleptoparasitism in fish-parasitic gnathiid isopods” 10.1007/s00436-018-6152-8

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## General introduction

Parasitism is a type of interaction between two organisms in which one organism benefits from the other on the latter's cost. Numerous sub-types of parasitism have been recognised, yet there is no concise, strict terminology available that provide a clear criteria for identifying between subtypes. For philosophical reasons, it might be impossible to provide such a frame (Minelli et al. 2006; Haug 2018). Still, it is worth discussing the use of certain terms for describing observed organismic interactions, just to avoid possible misunderstanding.

For this reason, it is necessary to comment on the applied terminology in a recent paper by Shodipo et al. (2018). The authors report on a unique case of interaction between con-specific isopodan crustaceans parasitising on fishes: parasitic gnathiid crustaceans feeding on the blood meal of other gnathiids. This observation is of crucial importance concerning the biological interaction, as it drastically expands the behavioural repertoire of parasitic isopodan crustaceans. We feel that the use of terminology in Shodipo et al. (2018) might be misleading and needs to be commented on. Throughout the publication, including the title, the observed behaviour is referred to as “kleptoparasitism” by Shodipo et al. (2018). We disagree on the idea that the observed behaviour should be regarded as kleptoparasitism, based on the criterion provided by the authors: “the act of one organism

stealing food from another”. While we are in agreement regarding this conception of kleptoparasitism, the phenomenon observed and recorded in Shodipo et al. (2018) should in our view be understood as the symbiotic relationship of hyperparasitism rather than kleptoparasitism.

## Parasitism concepts

Parasitism is in general a type of syn-vivo interaction between two organisms. Many different criteria have been applied to identify an interaction as parasitic. These criteria from different sources often provide “grey areas” or a limitation of information. For example:

The Oxford Dictionary of Biology (Martin and Hine 2008, p 477), describes parasitism as “an association in which one organism (the parasite), lives in, or on the body of another (the host), from which it obtains its nutrients”. This way of describing parasitism would mean that many plant-living and feeding insects (Schoonhoven et al. 2005) should not be interpreted as “herbivores” but as “parasites”. Similarly, Price et al. (1986) describe parasites as “species that draw their food resources from the live bodies of another species”. This definition would also suggest that many herbivorous insects would be considered as representing parasites, and would, in this case, include the lifestyle of mosquitoes and comparable insects. Many authors tend to refer to the behaviour of mosquitoes as “micro-predation”. The weakness of this concept is that the term “micro-predator” can also be used to refer to small-sized predators such as raptorial water fleas, raptorial mites or dwarf whip scorpions. Both concepts of parasitism provided by the Oxford Dictionary of Biology and that of Price et al. (1986) do not account for the duration the parasite has to spend on the host.

To avoid the confusion, it is important to stress the time aspects that lack in common descriptions of parasitism. Mosquitoes should rather be referred to as “temporary parasites”, in contrast to the example of the human body lice

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*Pediculus humanus humanus* Linnaeus, 1758, which are referred to as “permanent parasites” (Kirkness et al. 2010). Smith and Smith (1999) conceptualised parasitism as the “relationship between two species in which one benefits while the other is harmed”. In this association, the host is usually not killed directly. In contrast, a parasitoid is an “insect larva that kills its host by consuming the host’s soft tissues before pupation or metamorphosis into an adult”. This conception of a parasitoid by Smith and Smith (1999) implies that only insect larvae qualify to be parasitoids, excluding all other animal groups and other life stages. Olsen (1974) provides, to our opinion, the most inclusive conception of parasitism as “a way of life in which one species, the parasite, living in or on another species, the host, gains its livelihood at the expense of the latter”. Olsen (1974) continues that parasitism is the symbiotic relationship in which the parasitic symbiont is physiologically dependant on the host in terms of habitat and sustenance. The importance is that the parasite always causes some degree of damage to its host. Still, also this conception lacks a relation to the time of interaction. Levinton (2014) provides a comparable conception of parasitism as “members of one species live at the expense of individuals of another, without consuming the hosts totally as food and thereby killing them”.

## Parasite categories

Many sub-categories of parasitism have already been established. Parasites can be differentiated depending on the position that they occupy on the host (ecto- or endoparasite) or the size of the parasite (macro- or microparasite; see Olsen 1974; Smith and Smith 1999; Rohde 2005; Levinton 2014). Olsen (1974) provides the distinction in grouping of parasites on a temporal basis, thus, including the time aspect. Temporary parasites represent those that only visit a host in search of food, after which they abandon the host. Stationary parasites are those that spend a certain amount of time on the host during a developmental stage. These stationary parasites can further be divided into two groups, those that stay with the host for only a part of their development (periodic parasites), and those that stay with the host for the whole duration of their lifecycle (permanent parasites). Many alternative types of parasitism can be differentiated; nevertheless, in this comment the focus is on two specific types, which are of importance in the context of the report by Shodipo et al. (2018):

- 1) In some cases a parasite can also become the host of another parasite. This association of “a parasite that lives in or on another parasite” is referred to as hyperparasitism (Martin and Hine 2008). Labruna et al. (2007) provide the explanation of hyperparasitism as “a tick feeding directly on another tick”.
- 2) The term kleptoparasitism addresses a behaviour that can be described as “a bird, insect, or other animal which habitually robs animals of other species of food” (as in English Oxford Living Dictionary 2018). Tylianakis et al. (2006) refer to kleptoparasites as those that “feed on the host’s food resources”. This type of behaviour is not immediately recognised as parasitism in the strict sense, since many free-living organisms steal, makes use of, or simply benefit from the resources that another organism, of the same or different species, has acquired or collected. In this context of kleptoparasitism by Tylianakis et al. (2006), it would also include all cases of exploitation competition. Sivinski et al. (1999) explains that the period in between the collection of food, and the final consumption thereof, provides opportunity for kleptoparasites to exploit these resources.

Cases of behaviour that have been referred to as kleptoparasitism and hyperparasitism have been recorded for various different animal groups:

- 1) Examples of kleptoparasitism can be interspecific, such as between species of food-storing spiders and insects that are susceptible to the dipteran thief flies (Sivinski et al. 1999) and between hyenas attempting to potentially steal the kills of wild dogs (Carbone et al. 2005). This association can also be intraspecific, such as the “finder’s share” tactics of capuchin monkeys that exploit food collected by another individual (Di Bitetti and Janson 2001) or kelp gulls that attack each other in order to steal food (Bertellotti and Yorio 2001).
- 2) Hyperparasitism has also been recorded in inter- and intraspecific associations. Interspecific hyperparasitism is observed between mosquitoes as host with ectoparasitic mites (Werblow et al. 2015; Dos Santos et al. 2016), bacteria of the group *Wolbachia* (Sanogo and Dobson 2004), and the fungus *Trichoderma virens* on its host, the plant pathogenetic fungus *Rhizoctonia solani* Kühn, 1858 (Tu and Vaartaja 1981). Interspecific hyperparasitism has also been recorded for the parasitic isopodan species of the group Cryptoniscidae (Cymothoidea, Epicaridea), where specimens of *Liriopsis pygmaea* (Rathke, 1843) were found parasitizing on the rhizocephalan *Briarosaccus callosus* Boschma, 1930, which in turn parasitized on the false king crab *Paralomis granulosa* (Hombron & Jacquinot, 1846) (see Lovrich et al. 2004). An example of intraspecific hyperparasitism was recorded by Helmy et al. (1983) between individuals of the Egyptian tick, *Ornithodoros erraticus* Lucas, 1849, in conditions where they were attached and detached from their rodent host *Arvicanthis niloticus* (Geoffrey, 1803). Helmy et al. (1983) went further and provided additional terms for what they have described as intraspecific

hyperparasitism, as homoparasitism or conspecific parasitism. Sullivan (1987) provided the alternative terms of “autohyperparasitism” (intraspecific) and “allohyperparasitism” (interspecific). The question is in how far these terms will be generally understood or could instead simply be substituted by “interspecific hyperparasitism” and “intraspecific hyperparasitism”.

## The interesting case of parasitic gnathiid isopods

Isopodan crustaceans of the group Gnathiidae Leach, 1814 are ectoparasites of fishes. More precisely, larval stages of Gnathiidae are parasites, the adults seem to be non-feeding (Artim et al. 2015; Sikkel et al. 2006). In Shodipo et al. (2018), as well as in other previous publications, gnathiid isopodan crustaceans have been described as having an equivalent parasitic habit to that of mosquitoes and ticks. Other publications suggest that, due to their lifestyle, gnathiid crustaceans and their terrestrial equivalents should rather be referred to as “micropredators” (see above, as well as Penfold et al. 2008; Artim et al. 2015). As pointed out, we prefer to categorise this type of behaviour as “temporary parasitism”. Shodipo et al. (2018) reports and describes, for the first time, the interesting association in which unfed gnathiid crustaceans feed on the ingested blood meal of a fed gnathiid. This observation was referred to as kleptoparasitism by the authors. We disagree on this categorisation of parasitism and consider the described behaviour to be a case of hyperparasitism. The reasons for this preference are outlined in the following:

In order to better understand what it means to steal resources, as described for the association of kleptoparasitism, we need to first have a concept what “resources” are. Taylor (1926) outlines resources as “a composite of the goods (the foodstuffs) and the services in commerce and distribution through which these are made available for consumption”. The Cambridge dictionary (2018) agrees that resources are “something that can be used to help you” or “things of value such as money or possessions that you can use when you need them”. From the dictionary by Merriam-Webster (Resource n.d.), a resource is described as “a source of supply or support: an available means”. According to the above mentioned uses of the term, food resources refer to food and their nutrients that are available for consumption (e.g. in storage), which have not yet been used or consumed. Within a more ecological or biological context, Begon et al. (2006) describe resources as “entities required by an organism, the quantities of which can be reduced by the activity of the organism”. Levinton (2014) explains “a resource is any material whose availability or abundance in the natural environment can limit survival, growth, or reproduction”. These resources include food,

space, habitat and inorganic nutrients and all other resources (renewable or non-renewable).

A kleptoparasite steals the stored or collected food of another organism, *before* it could be used or consumed. Hyperparasites take some kind of nutrients, energy or form of substance from another organism, *after* it has been used or consumed (e.g. the blood and lymph of the host). This is supported by the statement of Olsen (1974), that “parasites rob the host of essential nutrients”. It is the opinion of the authors, that kleptoparasitism would most likely not be observed within parasitic species of the isopodan group Cymothoidea, simply because these parasites feed directly from their fish or crustacean host and have not shown any indication of storing or reserving their collected meal before consumption.

Since gnathiid isopods have been compared to their terrestrial parasitic counterparts mosquitoes and ticks, it is worth considering the terminology of publications dealing with the parasitic nature of mosquitoes and ticks. Labruna et al. (2007), as already stated, mention hyperparasitism as the term used for “a tick feeding directly on another tick”. Within the study of Helmy et al. (1983), the association between ticks and their rodent hosts has also been referred to as hyperparasitic. In the latter study, large ticks attracted the smaller unfed ones, similar to the attraction of unfed gnathiids to fed gnathiids in the observation of Shodipo et al. (2018). In addition, Helmy et al. (1983) provide a possible trigger for hyperparasitism: the overcrowded number of parasites and the lack or scarcity of hosts. This was also observed and reported by Shodipo et al. (2018), where the gnathiid parasites fed on each other in the case where both, fed and unfed individuals, were contained without any hosts.

## Concluding remarks

By considering the terminology and accompanying explanations of parasitism discussed above observations can sometimes cause misunderstandings and represent a limitation in certain aspects, depending on the context in which it is used. It is therefore essential to consider a wide variety of descriptions and characteristics of specific animal associations before categorising this interaction. The variation in uses of terms, such as in the case of mosquitoes, demonstrate that many apparent disputes can be solved by stepping back from the “naked” terms and look for the criteria behind the terms (Haug 2018). With regard to Shodipo et al. (2018), we suggest that the observations made, should be referred to as “hyperparasitism” rather than “kleptoparasitism”, based on the outlined criteria for both terms.

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