Precopulatory mate guarding in copepods

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Abstract

In many copepod species adult males clasp females for an extended period before transferring spermatophores. Clasping juvenile females (first to fifth copepodid inclusive) is interpreted as mate guarding and is shown to be widespread among podoplean copepods. It is distinct from copulation, which takes place only between adults and is often distinguishable from mate guarding by a difference in clasping posture.

Résumé

Chez de nombreuses espèces de Copépodes, les mâles adultes étreignent les femelles pour une assez longue période avant le transfert des spermatophores. Des mâles adultes étreignant les femelles juvéniles (du premier au cinquième stade de copépodide) représentent un phénomène fort répandu chez les Copépodes podopléens, et ceci est interprété comme "défense du conjoint". Ce phénomène est distinct de la copulation, qui caractérise uniquement les adultes; copulation et "défense du conjoint" se distinguent souvent par une différence dans la posture de l'étreinte.

Introduction

When sorting through samples of live copepods, or even fixed material, it is not uncommon to find pairs in which a male has a female firmly in its grasp. The male may hold the female with its geniculate antennule or antennules, its antennae, its maxillipeds, or with a combination of these limbs. This behaviour has acquired a number of names, including precopula, amplexus, precocious coupling and clasping. Ridley (1983) reviewed mating behaviour in a wide range of taxa and pointed out that the habit of attaching to a female until she is ready to copulate has often been confused with copulation (spermatophore transfer) itself. These two processes are distinct phases within mating and are referred to here as precopulatory mate guarding and copulation respectively. Male copepods are known to use their fourth or fifth legs to place the spermatophores on the female but other mechanisms are also common, such as the extrusion of spermatophores from the male genital apertures directly into position on the female genital somite.

In copepods, precopulatory mate guarding can be defined as the clasping by an adult male of a juvenile female at a moult stage before the adult. The grasping of an adult female by an adult male is classified as true copulatory behaviour. These two phases are separated by the last moult, at which the female becomes sexually mature and able to receive spermatophores. The posture of a clasping pair, especially the site at which the male grasps the female, is often different in these two phases. For example, in the Cyclopoida when males are mate guarding they typically attach to the dorsal surface of a female copepodid, whereas they attach to the fourth legs of the adult female in a ventral surface to ventral surface orientation when about to copulate. The interference to feeding and swimming of the female that would be caused by prolonged mate guarding in the ventral to ventral copulatory posture is avoided by the adoption of a different

posture during this phase. Adult males may be found clasping adult females in the mate guarding posture but this is interpreted as a transient phenomenon brought about by some delay in the male adopting the copulatory posture.

The occurrence of precopulatory mate guarding

Calanoida

There is no evidence that calanoids exhibit mate guarding (Ridley, 1983). Mating pairs, when observed, always involve adults of both sexes and such copulatory clasping is generally of short duration. An adult male diaptomid initially grasps the adult female with its geniculate antennule, then changes to holding on with its fifth leg (Watras, 1983), but both phases are of short duration and are rapidly followed by spermatophore placement.

Cyclopoida

The cyclopoids do not appear to exhibit a consistent pattern in mating behaviour. Precopulatory mate guarding certainly occurs in some parasitic cyclopoids. In the notodelphyid genus *Notopterophorus* both Thorell (1859) and Giesbrecht (1882) observed adult males attached to the dorsal surface of copepodid stage five females (Co.V). After these female copepodids moulted into adults the males reattached ventrally, to the fourth legs of the female, and spermatophore transfer took place. In many free-living cyclopids, such as *Eucyclops serrulatus* (Fischer, 1851) and *Tropocyclops prasinus* (Fischer, 1860), copulation is rapid and there is no precopulatory guarding (Hill & Coker, 1930).

However, Hill & Coker (1930) observed other species, such as *Orthocyclops modestus* (Herrick, 1883), in which adult males held on to the dorsal surface of Co.V females for a prolonged period until the females moulted. The males then changed position to the typical ventral to ventral orientation for spermatophore transfer (Fig. 4). Spermatophore transfer occurs in this position in the majority of cyclopoids because the single copulatory pore

through which the spermatophore discharges is located midventrally on the genital double somite. During copulation the male grasps the fourth leg of the female with its antennules, each of which is divided into three sections by two geniculations. At the proximal geniculation the antennule bends behind the female's leg and extends across the posterior surface to the ventral midline, at the distal geniculation it bends laterally to lie across the anterior surface of the leg.

Harpacticoida

Kern et al. (1984) analysed clasping behaviour in *Zausodes arenicolous* Wilson, 1932 and summarised a number of published observations on harpacticoids. Adult males of *Z. arenicolous* were found clasping all juvenile stages from the first copepodid (Co.I) to the fifth (Co.V) but not adult females. Itô (1970) found males of *Tigriopus japonicus* Mori, 1938 guarding all stages from Co.I to adult female. Lasker et al. (1970) recorded males of *Asellopsis intermedia* (Scott, 1895) clasping stages from Co.II to Co.V and the latter was the most frequent. Dahms (1988) illustrated an adult male of *Harpacticus uniremis* Krøyer, 1842 grasping a Co.III stage female. Most other records tabulated by Kern et al. (1984) involve males clasping Co.IV to adult females.

Males may grasp females around their caudal setae (Figs. 1 & 2), caudal rami, anal somite, fourth leg or by the posterolateral margins of the dorsal cephalothoracic shield (Lang, 1948). In the majority of these postures the males would be in the wrong position to transfer the spermatophore(s) to the copulatory pore(s) of the female, which lie midventrally on the genital somite or double somite, and must change grip just prior to transfer. Postures such as grasping the dorsal shield are associated with mate guarding (see Dahms, 1988: fig. 4A). Grasping the fourth leg, as found in members of the family Laophontidae, is a suitable position for spermatophore transfer.
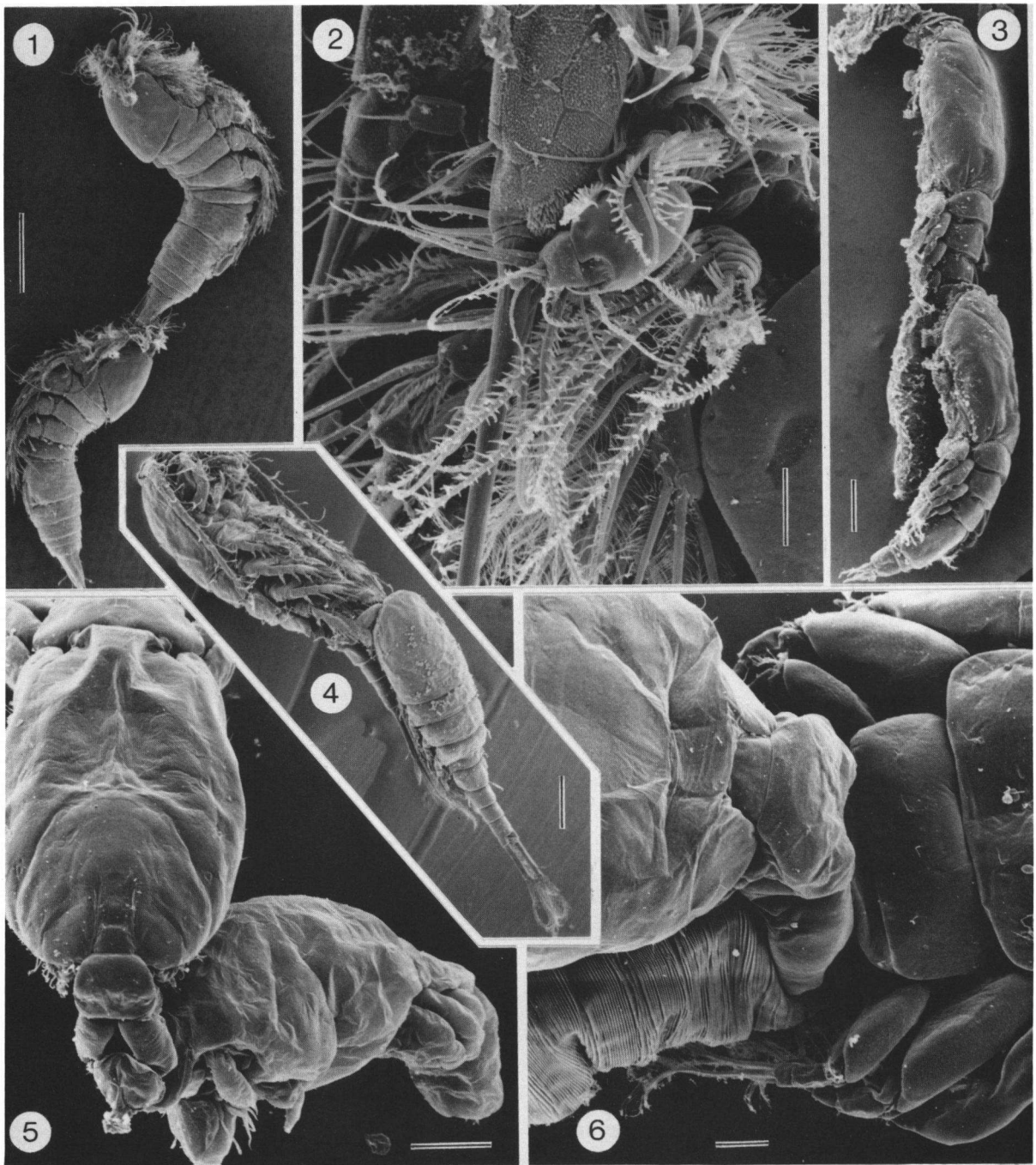
Figs. 1–6. 1. Adult male of *Canuella perplexa* clasping adult female (scale bar 250 μm); 2, Same, showing detail of antennulary clasping (scale bar 25 μm); 3. Adults of *Lernaeocera branchialis* in mating posture just prior to spermatophore transfer (scale bar 200 μm); 4. Mating pair of *Cyclops vicinus* Ulianine, 1875 showing male grasping fourth legs of adult female (scale bar 250 μm); 5. Adult male of *L. branchialis* guarding early copepodid stage female (scale bar 125 μm); 6. Detail of Fig. 3 showing antennary clasping at prosome-urosome boundary (scale bar 40 μm).

Poecilostomatoida

Do et al. (1984) record adult males of *Pseudomyicola spinosus* (Raffaele & Monticelli, 1885) clasping juvenile stages, from the third copepodid, as well as adult females. The orientation of the male and female during mate guarding is the same as during copulation. The adult male holds the dorsal surface of the female using either the antennae, or the maxillipeds or both. This position is suitable for spermatophore transfer because in all poecilostomatoids, except the Erebonasteridae, the openings of the seminal receptacles are located in the paired dorsal genital apertures of the female.

Siphonostomatoida

The life cycles of these parasites may be abbreviated and the developmental stages are often modified, but precopulatory mate guarding is still a common phenomenon. Ho (1966) found adult males of the pennellid *Cardiodectes* sp. clasping all developmental stages from the single copepodid, through the three attached chalimus stages, to the adult female. Chalimus III was the stage most frequently involved (44% of the observations). In *Lernaeocera branchialis* (Linnaeus, 1767), a pennellid with four chalimus stages, adult males use their antennae to grasp early chalimus stages in the vicinity of their frontal attachment apparatus (which is not moulted with the rest of the exoskeleton) when exhibiting mate guarding (Fig. 5), but hold adult females around the prosome-urosome junction (Fig. 3) when preparing to copulate. The caligid *Lepeophtheirus pectoralis* (Müller, 1776) has a life cycle including 1 copepodid, 4 chalimus, and 2 preadult stages preceding the adult. Adult males are found clasping all stages from chalimus IV to the adult female but the stage most commonly involved (71%) is the second preadult female (Boxshall, 1974).

Male appendage morphology

The appendage or appendages used by the male for grasping the female during mating are in general strongly sexually dimorphic. In male calanoids this is either the antennule or the fifth leg, in male cyclopoids and harpacticoids the antennules, in male poecilostomatoids the maxillipeds and in male siphonostomatoids the maxillipeds or antennae (Fig. 6), or both. The extreme case of such dimorphism is the loss or gross reduction in the female of a pair of appendages used primarily for clasping by the male. For example, adult females of *Pseudomyicola spinosus* have only a vestige of the maxilliped whereas in the male it is a well developed raptorial limb.

Discussion

Ridley (1983) considered the predictability of sexual receptivity in the female to be the major factor controlling the incidence of mate guarding in a wide range of taxa. In most female copepods sexual receptivity is predictable because it is linked to the moult cycle, the female becoming sexually mature and ready to receive spermatophores immediately after the terminal moult (from the last copepodid stage). In many podoplean copepods one copulation appears to be sufficient for the entire reproductive output of the female, although in some there may be several copulations during a receptive period after the final moult. In some parasitic podopleans the single copulation or receptive period is followed by a postmating metamorphosis which prevents remating. The widespread occurrence of precopulatory mate guarding in podoplean copepods is, therefore, consistent with Ridley's conclusion.

There appears to be no precopulatory mate guarding amongst the calanoid copepods. Watras (1983) demonstrated that female diaptomids frequently oscillate between gravid and non-gravid condition and that remating during the gravid phase of the life cycle is required for each successive clutch of eggs produced. In an oscillating cycle of this sort, receptivity is less predictable. It is possible that those podoplean copepods in which remating occurs, such as *Oithona* (see Uchima, 1985), may show a similar receptivity pattern. It is probable that these copepods, which typically have a very

low proportion of males, have males that produce spermatophores iteratively and mate with more than one female. However, these are the copepods that do not exhibit mate guarding behaviour.

The evolution of mate guarding by male copepods presumably confers some selective advantage on them, increasing their reproductive success. The nature of this selective advantage is difficult to identify because so little is known about the reproductive biology of male copepods. The fecundity of female copepods and the iteroparous nature of egg laying is now well documented but few data are available on male reproductive biology, particularly on whether or not an individual male can produce spermatophores sequentially over an extended period of time. Mate guarding is interpreted as a male mediated behaviour but it is possible that being mate-guarded confers some selective advantage on the female. Any such advantage would have to outweigh the disadvantages of carrying a male round whilst feeding and moulting.

An obvious advantage to a male that produces spermatophores iteratively would be if it could expect to mate more rapidly (and therefore more often) by guarding a female until it is receptive than by searching for receptive but unmated females in the population. Guarding represents a significant investment of time by the male although selection of later copepodid stage females would lessen this investment. If a male mates only once in its lifetime then every unmated female is a potential mate, including juvenile stages. Given a low probability of encountering a receptive female it may be to the benefit of the male to guard any unmated female until she becomes sexually receptive. The sex ratio is likely to be a significant factor here since mate guarding would clearly be advantageous if potential mates are in short supply. The preference for unmated rather than mated females could be explained by a variety of other factors, sperm competition for example, but insufficient information is available on male reproductive physiology to allow such hypotheses to be adequately tested.

There is good evidence that pheromones are involved in copepod mate seeking behaviour (Katona, 1973). Precopulatory mate guarding is widespread in podopleans and it most commonly involves copepodid stage females. If mate-seeking behaviour is mediated by pheromones in these copepods then the pheromone-producing organs must be functional in the copepodid stages.

Acknowledgement

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