HORIZONS

Copepod mating: chance or choice?

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Mate choice is common in most animals, but the issue has largely been ignored in regard to pelagic copepods—the most abundant zooplankton group in the oceans. Contemporary demographic models of copepods assume that all encounters lead to successful copulation and viable egg production. We revisit the subject of copepod mating biology in the framework of sexual selection theory. We discuss, and point to, examples that suggest mate choice in both sexes. Sexual selection theory may add an important dimension for understanding copepod population dynamics and potentially lead to renewed interpretations of the diverse copepod behaviours and life histories. In addition, the range of mating strategies in copepods represents a rich, but unexplored, source of information for general behavioural ecologists.

INTRODUCTION

Despite their ecological importance, the issue of sexual selection in pelagic copepods has received little attention. This may partially be due to the assumption that reproduction in copepods is mainly encounter limited. Recently, mate-encounter processes, and in particular mate search behaviour of males, have been thoroughly studied (e.g. Doall *et al.*, 1998; Tsuda and Miller, 1998; Bagøien and Kiørboe, 2005a, 2005b). These studies document sophisticated mating behaviours, including male tracking of cues produced by females, elaborate dances and female escape behaviour (e.g. Tsuda and Miller, 1998; Kiørboe *et al.*, 2005).

In animals, reproductive investment in gametes or other resources provided to offspring often differs between the sexes. Asymmetric parental investment generally predicts that the sex investing fewer resources (typically males) is limited by the availability of the sex investing more (typically females) (Trivers, 1972). As a consequence, males compete for access to fertilization and females exert mate choice and select among available males. In some systems, sex roles are reversed with males providing more resources and choosing among females (Vincent *et al.*, 1992). Alternatively, both sexes may be choosy (Jones and Hunter, 1993), or sex roles can be plastic and change temporally (Forsgren *et al.*, 2004).

Copepod species differ with respect to sex-specific reproductive investment. In calanoids, the highly fecund broadcast spawners lack parental care, whereas the less fecund egg carrying species invest more per egg (cf. Kiørboe and Sabatini, 1994). There are also interspecific differences in male investment per mating, both in terms of energy and risk. This is reflected in large variation in spermatophore size (Mauchline, 1998), investment in geniculate antennae and a fifth chealate leg for clasping females (e.g. Ohtsuka and Huys, 2001), as well as in mate search activity *per se* (Kiørboe and Bagøien, 2005; Kiørboe, 2006).

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The importance of sexual selection is density dependent, with more potential for mate choice under high mate encounter rates (Kokko and Rankin, 2006). The intensity of sexual selection also depends on the number of receptive females relative to the abundance of competing males (i.e. the operational sex ratio, Emlen and Oring, 1977). Adult sex ratios in copepods are often female biased (reviewed in Hirst and Kiørboe, 2002; Kiørboe, 2006). This sex skew is largely attributed to lower survival of males, resulting from their motility patterns and speed (Kiørboe, 2006). However, adult sex ratios may not represent a good proxy for the operational sex ratio as already mated females may not be receptive or males may temporarily have run out of spermatophores.

Copepod mating was recently incorporated into a demographic model (Kiørboe, 2006) aimed at understanding how adult concentrations, mating behaviour and sex ratios influence population dynamics in pelagic copepods. A central assumption in Kiørboe's (Kiørboe, 2006) model is that all encounters lead to copulation and production of viable eggs. However, aspects of copepod mating strategies, including morphological, physiological and behavioural traits, suggest that encounters between fertile mates do not necessarily lead to successful copulations. Here, we revisit the subject of mating of pelagic copepods in the framework of sexual selection theory.

the oceanic copepod *Pleuromamma piseki*, females and males with ripe spermatophores migrate to shallow habitats during night, although males without ripe spermatophores reside deeper (Hayward, 1981). In similar ways, the coastal species *Acartia clausi*, *C. typicus* and *T. longicornis* form dense swarms, reaching concentrations of several thousands per litre (direct observations by E. Selander, personal communication). At least for *C. typicus*, the swarms are male dominated and the few females present often have spermatophores attached. Such swarms resemble leks, which are common in insect, bird and fish species (Höglund and Alatalo, 1995).

Aggregations may also result from sex-specific migration and distribution, common among copepods diapausing as adults or in near adult stages. Males in many such species tend to migrate earlier and also position themselves within relatively narrow depth intervals (cf. Miller and Clemons, 1988; Miller *et al.*, 1991; Spiridonov and Kosobokova, 1997; Heath, 1999). Hence, receptive females pass searching males on their way to the surface (Miller *et al.*, 1991; Spiridonov and Kosobokova, 1997; Heath, 1999), or even when migrating down to enter diapause (Miller and Clemons, 1988)—an adaptation in males to enhance female encounters. Protandrous arrival times are commonly observed in several other arthropods and birds (Morbey and Ydenberg, 2001).

ENCOUNTER LIMITATION OF COPEPOD MATING?

The dilute planktonic environment offers challenges to small copepods trying to locate each other as the probability of randomly bumping into potential mates is minute. It has therefore been argued repeatedly that copepod mating is encounter limited (e.g. Buskey, 1988; Kiørboe and Bagøien, 2005; Kiørboe, 2006). However, copepods have various adaptations that enhance location of mates. Females attract males by transmitting chemical signals through plumes (e.g. *Pseudocalanus elongatus*) and trails (e.g. *Centropages typicus*, *Calanus marshallae*, *Temora longicornis*), or by using hydrodynamic signals (e.g. *Acartia tonsa*, *Acartia hudsonica*) (review in Bagøien and Kiørboe, 2005a). When correctly perceived and interpreted, these signals allow males to search efficiently through large volumes of water ($10-1000s$ L day^{-1}, Kiørboe and Bagøien, 2005a; Kiørboe, 2006).

Other adaptations to reduce encounter limitations include pre-copulatory mate guarding (Burton, 1985; Uchima and Murano, 1988), aggregations and swarming (e.g. Ambler *et al.*, 1991; Tsuda and Miller, 1998). In

SINGLE OR MULTIPLE MATING?

The potential for being selective typically declines with the decreasing availability of mates. Many copepods, including *Calanus* spp. (e.g. Marshall and Orr, 1955) are supposedly restricted to one single mating event that fertilizes all eggs. Similarly, in several species one spermatophore is probably enough to fertilize (all?) eggs for $\sim 2-2.5$ months (e.g. *A. clausi*, Uye, 1981; *Calanus* spp. Marshall and Orr, 1955; *Eurytemora affinis*, Katona, 1975) or up to 10 successive egg sacs (*Pseudocalanus* spp., Corkett and Zillioux, 1975). In other species (e.g. *Centropages* spp., *E. affinis*, *Temora stylifera*, *A. tonsa*) females lack seminal receptacles and thus the ability to store sperm except in the spermatophores (Ohtsuka and Huys, 2001). They therefore need to replenish sperm supply continuously (e.g. *A. tonsa*, Wilson and Parrish, 1971; *T. stylifera*, Ianora *et al.*, 1989). The number of matings required may depend on the age of the female at first mating, explaining the contradicting observations on, for example, *E. affinis* and *Acartia* spp. (Mauchline, 1998).

In species where a single spermatophore is sufficient to fertilize all eggs, the adaptive value of female

multiple mating is less obvious. Mating with several males may potentially provide direct advantages or indirect benefits through the acquisition of good or compatible genes to offspring (reviewed in Jennions and Petrie, 2000). Females may ensure fertilization or obtain various material resources from several males. In some insects, males transfer extra nutrients in the seminal fluid or the spermatophore that females use for egg production (Andersson, 1994). For instance in long-wing butterflies (*Heliconius*), males supply chemicals with their spermatophores that defend mothers and offspring (Cardoso and Gilbert, 2007). Material benefits from spermatophores have as far as we know not been explored in copepods. Reports, however, suggest that copepod spermatophores, such as in *Metadiaptomus* spp., contain various substances (Defaye *et al.*, 2000).

The predictability of the environment and the ability to discriminate between various males based on their quality may determine whether single or multiple matings are adaptive for females. If a female possesses good information and is able to recognize high quality males (cf. Goetz, 2004), she may choose to mate only once. However, if the probability of encountering such males is low, she may first mate indiscriminately with a lower quality male, and later with a better male to whom she allocates most fertilization (Yasui, 1998) (see also the section Post-copulatory mate choice and paternity analyses below). If, however, females possess little information on male quality, females may benefit from multiple mates as a bet hedging strategy.

While some copepods only place one spermatophore per mating, others place several (reviews in e.g. Mauchline, 1998). Females with multiple spermatophore attachments have been observed in many species, including species where females supposedly only mate once and where males only place one spermatophore per mating (e.g. *Calanus* spp.) (e.g. Gibbons, 1933, in Mauchline, 1998). There are also observations of a male *Oithona davisae* that waited for another male to finish copulation, after which he jumped at the female (Uchima and Murano, 1988). Such records suggest that although a single male may successfully fertilize all eggs of a female, multiple matings and paternities might be widespread also in species where females are traditionally believed to mate only once (Todd *et al.*, 2005).

MATE CHOICE

Copepod mating may be visualized as a ladder consisting of steps of encounter, pursuit, capture and copulation (Buskey, 1988). In the copulation step, the male places a flask like spermatophore onto or close to the female's genital opening, and the sperm are subsequently transferred from the spermatophore into the seminal receptacle in many species (reviews in Blades-Eckelbarger, 1991; Ohtsuka and Huys, 2001). The male either invokes the female to mate willingly or simply attacks her. Below we revisit some examples of behaviour that suggest that both sexes assess and choose among available mates. Mate choice in copepods may occur in both pre- and post-copulatory stages (e.g. Palmer and Edmands, 2000).

Complicated pre-copulatory dances

Sophisticated pre-copulatory behaviour is a common component of mate choice and includes songs, calls and dances typically performed by the advertising sex (Andersson, 1994). Copepods exhibit various examples of such behaviours. The best example is *P. elongatus* in which both sexes engage in a pre-copulatory dance when the male has located the female (Kiørboe *et al.*, 2005). During the dance, which may last for more than 5 min, the couple makes repeated contact every $10-20$ s (Kiørboe *et al.*, 2005). Sometimes the female performs short escape jumps (Kiørboe *et al.*, 2005). Species that use hydromechanical signals for mate recognition also engage in a long series of communicative hopping before copulation (e.g. *A. tonsa*; Bagøien and Kiørboe, 2005b). In *O. davisae*, the male hops between pheromone patches generated by hopping chemically advertising females (Kiørboe, 2007). The male either captures the female or looses the track (Kiørboe, 2007). However, as exemplified with *O. davisae*, it is often difficult to distinguish mate search from courtship.

Male behaviour is commonly directed at a specific female, and this courtship may represent a way of checking female mating status to avoid wasting valuable spermatophores. In addition, both males and females may use courtship performance to assess the quality of mates. Pre-copulatory dancing may also serve an important species recognition function (Andersson, 1994, p. 211), as fruitless inter-specific mating occurs in several copepods (e.g. Jacoby and Youngbluth, 1983; Maier, 1995).

Escaping

Females sometimes escape pursuing males, and this occurs in species that use both chemical and hydrodynamic signals to advertise their readiness to mate (Table I). Despite the complex courtship dances of *C. marshallae*, most ended without copulation as the female typically abandoned the male with intensive escape jumps (Tsuda and Miller, 1998). In other species,

Table I: Some species where female escape from pursuing males has been observed

Species	Escape behaviour	Reference
Acartia tonsa	Calm parting by swimming	Bagøien and Kiørboe (2005b)
Calanus marshallae	Jump away from male	Tsuda and Miller (1998)
Centropages typicus	Jump away from male	Bagøien and Kiørboe (2005a)
	Shake off male	T. Kiørboe, personal communication
Oithona davisae	Jump away from male	Kiørboe (2007), T. Kiørboe, personal communication
	Shake off male	T. Kiørboe, personal communication
Pseudocalanus elongatus	Short jumps away from male	Kiørboe *et al.* (2005)
Temora longicornis	Jump away from male	Doall *et al.* (1998)

females also shake off males that have attached themselves to the females' body (Table I). The fact that females first employ pheromones to attract males (review in Bagøien and Kiørboe, 2005a) and then escape when encountered (Table I) suggests female mate choice. Female escape behaviour also suggests a conflict of interest between sexes over mating (Arnqvist, 2004). Males with low investment in offspring may benefit from trying to mate at every opportunity (if they have available spermatophores). In contrast, females may benefit little from additional matings, and may therefore try to avoid excessive males.

Most escape observations (Table I) are qualitative, and escape frequencies have unfortunately rarely been quantified (but see e.g. Maier, 1995). Because most observations of mating are made in high abundances of both males and females, we know little about the plasticity of rejection rates as a function of, for example, sex-ratio or mate encounter rates.

As a potential counter to female escape behaviour, males of many calanoids have geniculate antennae and a fifth, sometimes chelate, leg that they use to catch and hold the female (cf. Ohtsuka and Huys, 2001). Interestingly, genera that lack geniculate antennae include *Pseudocalanus* and *Calanus*, both of which engage in elaborate dances (Tsuda and Miller, 1998; Kiørboe *et al.*, 2005).

Stroking

In some copepods, males exhibit elaborate behaviours directed towards getting the female to accept a spermatophore placement. In some species (e.g. *Labidocera aestiva*), males use their fifth leg to stroke the ventral surface of the female's genital segment prior to copulation (Blades and Youngbluth, 1979). Such persuasive actions typically exist in mating systems with female choice (Andersson, 1994). Pre-copulatory behaviour may also be tied to post-copulatory choice of sperm, i.e. cryptic female choice (see Eberhard, 1996, and below), if females are more likely to store and use sperm from males that first provide the right stimulation.

Pre-copulatory mate guarding

Many cyclopoid and harpacticoid copepods from environments ranging from the intertidal to the pelagic engage in pre-copulatory mate guarding. Males attach to unripe females, usually at their CV stage, and hold on until their final moult (e.g. Burton, 1985; Boxshall, 1990; Frey *et al.*, 1998). For males, such mate reserving behaviour comes at costs of missed mating opportunities and increased predation risk. Males exert mate choice based on female maturity status (e.g. Burton, 1985; Uchima, 1985): males guard females as young as CIII, but they prefer older virgins and may switch to an older female if one appears later on (Burton, 1985).

Post-copulatory mate choice and paternity analyses

In many animals, polyandrous females are able to bias fertilization of eggs towards preferred males. For instance, females that are capable of detaching unwanted spermatophores may exert post-copulatory mate choice directly (Defaye *et al.*, 2000). Such or similar findings in copepods would not be surprising given the wide range of mechanisms for cryptic female choice displayed in other animal groups, such as insects (reviewed in Eberhard, 1996). Cryptic choice often reveals as biases in paternity, but to our knowledge genetic studies of paternity have not been performed in pelagic copepods. Todd *et al.* (Todd *et al.*, 2005), however, showed that in an ectoparasitic copepod where females were believed to mate only once and also engage in complex mate guarding, several males actually sired offspring from single clutches.

SPERM COMPETITION

Sperm competition is common in many animals (e.g. Møller, 1991; Stockley *et al.*, 1997) and was originally interpreted from the perspective of male–male competition (Parker, 1970). Sperm competition can be manifested as strategies aiming at out-competing others in sperm numbers, longevity or swimming performance (Snook, 2005). Sperm competition has to our knowledge

not been studied in copepods. Calanoids generally have simple spermatophores, which are similar in form (reviews in Blades-Eckelbarger, 1991; Mauchline, 1998). However, some multiple maters (e.g. Centropagidae and Pontellidae) have more complex spermatophores (reviews in Blades-Eckelbarger, 1991; Mauchline, 1998), which may possibly be adapted to post copulation sperm competition.

A potential adaptation to sperm competition also includes cases where copepod males place two spermatophores per copulation, where the second attachment may serve as a block to re-mating (Jacoby and Youngbluth, 1983). Males may also strive to reduce sperm competition by actively guarding the female after copulation to limit the access of other males. Some harpacticoid copepods (*Tisbe* spp., *Paramhisella fulvofacida*) engage in prolonged mate guarding during transfer of sperm from the spermatophore (Dürbaum, 1995). Males may also remove spermatophores attached by other males to ensure paternity, a tactic employed by ground beetles (Takami, 2007).

REPRODUCTIVE INVESTMENT

Mate choice can be performed by one sex only, or be important for both sexes to various degrees, typically depending on relative investment in offspring. In many animals, the reproductive investment differs between sexes, and is typically higher for females. Although egg production involves major costs for females, spermatophore production may involve comparable energetic investments for male copepods (Mauchline, 1998). Spermatophore volume scales to body volume, and is on average $\sim0.5\%$ of the body volume, but inter-specific variance is very high, especially in small species (Mauchline, 1998). Spermatophore size also depends on nutrient availability, and males can in some cases vary their investment depending on resource availability (i.e. *Macrocyclops albidus*, Sivars-Becker, 2004). High male investment into spermatophores suggests that nutritious proteins, potentially manipulative hormones or other chemical substances may be supplied with the spermatophore, as in many insects (Arnqvist and Nilsson, 2000).

Spermatophore production may limit the number of matings that a male can perform (Hopkins, 1982; Kiørboe, 2007), as published spermatophore production rates are low; only $0.1-3\ \mathrm{day}^{-1}$ (Hopkins, 1982; Ianora and Poulet, 1993; Ianora *et al.*, 1999; Kiørboe, 2007). Even at very low female concentrations, males typically encounter several females per day (search volume $10-1000\mathrm{s}\ \mathrm{L}\ \mathrm{day}^{-1}$, Kiørboe and Bagøien, 2005), suggesting that spermatophore production may be more limiting than encounter *per se*. Limiting mating capacity (or

spermatophore production) was recently documented for *O. davisae* (Kiørboe, 2007). High relative investment in spermatophore production combined with few adult males per female (Hirst and Kiørboe, 2002) may therefore increase the potential for male choice. Life histories where sperm production is costly or time-consuming, for instance, in species that rely entirely on energy stores for reproduction (e.g. *Neocalanus* spp., Miller *et al.*, 1984, Saito and Tsuda, 2000) are possible candidates for male choice. As female fecundity also scales with energy stores in these species, males with costly spermatophore production should selectively choose females with large stores.

ORNITHOLOGY FOR COPEPODOLOGISTS

Long ago, Hutchinson (Hutchinson, 1951) pointed out through "a number of disconnected facts of considerable evolutionary significance" how behaviour (e.g. selective feeding) and life history strategies (e.g. clutch size) in copepods were relevant to general ecology. Similarly, we have highlighted examples in the recent literature that calls for an ornithologist's perspective on the sexual behaviour of copepods. It appears that sexual selection is more important than it has been given credit for in the copepod literature, and that obviously it is an integral part of the life history strategies and behaviour of copepods. Below we list some research questions waiting to be solved.

Copepods: a general model system for mating behaviour?

Copepods belong to a large, diverse and well-studied group that inhabits most aquatic habitats. The group displays a wide range of mating types including presence or lack of sperm storage capacity, feeding and non-feeding males, mating aggregations and lekking, pre- and post-copulatory mate-guarding or no mate guarding, and free spawning and egg bearing females. This diversity could reveal patterns useful for testing general theories of mating behaviour. In addition, copepod life histories are diverse and shaped by a range of factors (e.g. Miller *et al.*, 1984; Varpe *et al.*, 2007). Sex-specific life history traits such as phenology, energy allocation and habitat use are common, but often a neglected perspective in life history studies and theoretical models of copepods (e.g. Varpe *et al.*, 2007). Selection pressures from mate choice act on a variety of traits including morphology of genitals, antennae, fifth leg and mouth parts (Ohtsuka and Huys, 2001), spermatophore

structure (Blades-Eckelbarger, 1991), and chemical compounds involved in sexual communication (e.g. Frey *et al.*, 1998). More integrative research summarizing patterns of co-evolution in morphology, life history traits and mating behaviours would be instructive.

What is the male reproductive investment?

While copepod females and their allocation of energy into egg production have been thoroughly studied, our insight into male reproductive investment, for example, in spermatophore production and morphological features is limited (but see e.g. Ianora *et al.*, 1999). Fertilization limitation has received little attention, despite its potentially large implications for population dynamics (but see Hopkins, 1982; Kiørboe, 2007). For instance, the much debated occurrence of sterile eggs in copepods might well be due to a combination of limiting spermatophore production and a shortage of males (Kiørboe, 2007). If so, what makes males the limiting sex? Exploring differences in energetic costs of spermatophore production may provide clues to the role of males in limiting female fertilization. Also, do copepod males provide more than sperm in their sometimes surprisingly large spermatophores? In insects, protein, manipulative hormones or chemical gifts (Cardoso and Gilbert, 2007) are transferred to females in the ejaculate or spermatophore (e.g. Arnqvist and Nilsson, 2000). Better knowledge of the content of spermatophores may reveal how female choice influences male reproductive investment.

To what extent do females engage in multiple matings?

Do single clutches of eggs have multiple paternities? Our understanding of copepod mating would benefit from the use of contemporary molecular methods. Genetic fingerprinting represents a useful tool to assess the extent of female polygamy in copepods (cf. Todd *et al.*, 2005), as well as the degree of post-copulatory female choice (cf. Takami, 2007). The current assumption that females of many copepod species mate only once strikingly parallels beliefs held by ornithologists before the use of molecular paternity analyses altered the perception of widespread monogamy to frequent promiscuity in birds (Griffith *et al.*, 2002). The fact that many female copepods actively attract males using chemical signals suggests a benefit to females of enhanced male encounter rates. When should females use pheromones to advertise for males? Is female chemical signalling plastic and inducible allowing females to adjust pheromone signalling based on male density or mating frequency? Combining studies on proximate mechanisms with studies on the functional or evolutionary drivers of these behaviours would yield answers to such questions. Copepods may be a good system for further theory developments since encounter-models are already well advanced (e.g. Kiørboe and Bagøien, 2005; Visser, 2007).

What are the costs and benefits of multiple matings?

We know little about the evolutionary trade-offs of mating frequency in copepods. The costs of high mating frequency may be associated with risks of predation, parasite infection and energy losses, whereas benefits may include steady supplies of sperm, genetic variability in offspring or material benefits provided in spermatophores. The adaptive value of female multiple matings is debated intensively among behavioural ecologists (e.g. Arnqvist and Nilsson, 2000). Copepods may have a story to tell.

Does sexual selection matter?

While ornithologists consider sexual selection to be interesting in its own right, copepodologists often focus on more applied questions related to ocean productivity, fisheries and the cycling of matter in a changing global environment. Population dynamics emerge from individual behaviour, which is formed through natural and sexual selection that do not necessarily maximize population growth rates or stability. It is therefore key to understand the discrepancy and sometimes decoupling between demography and individual fitness that is frequently exposed in mating systems (Kokko and Rankin, 2006). The implications of mate choice and sex-specific reproductive investment on processes at the population level deserve theoretical and experimental attention. We believe progress will be made by simply starting to interpret available and future observations against the background that mate choice is a possibility also in copepods.

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