Mating Behaviour and Copulatory Mechanism in the Scorpionfly Neopanorpa longiprocessa (Mecoptera: Panorpidae)

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Abstract

 Sexual conflict during copulation may drive morphological and behavioral evolution in insects. Although nuptial feeding behaviour is well studied in Panorpa, whether this behaviour is universal in Panorpidae remains unknown. The scorpionfly Neopanorpa longiprocessa Hua & Chou, 1997 was investigated for its mating behaviour, functional morphology of the natal organ, and external genitalia using light microscopy and scanning electron microscopy. The results show that the mating behaviour is not associated with nuptial feeding in N. longiprocessa. The morphological basis of this non-nuptial copulation is likely related to the developed natal organ of the male. The natal organ serves a function to seize wings of the female during copulation. Only males that succeed in seizing the female with the natal organ are able to establish genital contact and copulate. The male genitalia exhibit distinct species-specific modification. The epandrium (tergum IX) has a pair of dorsal processes to control the abdominal end of the female. These results indicate that nuptial feeding is not a universal behaviour in Panorpidae. Presumably, these grasping apparatuses compensate the scorpionflies that fail to provide nuptial gifts, as exemplified by N. longiprocessa.

Introduction

 Sexual conflict over control of copulation and fertilization may drive the evolution and diversification of genitalia and non-genital contact structures of insects [1–4]. In males, these modified structures are used to grasp, seize, or stimulate the female, and improve male copulation success through overcoming female resistance [5,6]. These specialized traits diverge rapidly over evolutionary time, and are considered one of the most general evolutionary trends in insects [2–4,7].

 Many behavioral adaptations, such as nuptial feeding, are also involved in mediating sexual conflict [8]. Nuptial feeding refers to nutrient transfer from the male to the female during courtship and/or copulation [8,9]. In insects the nutrient could encompass any form of edible gifts, including preys, glandular products, or even male body [9,10]. There are two main hypotheses for the function of nuptial gifts: as paternal investment or as mating effort [11,12]. As mating effort, the nuptial gifts provided by males could enhance male control of copulation by mediating female resistance [8].

 Panorpidae in Mecoptera are characterized by various nuptial feeding behaviours in their courtship and copulation [13–15]. The males of Panorpa benefit from nuptial feeding being increasing their paternity, such as prolonging copulation, increasing sperm transfer rate, decreasing female remating rate, and increasing female egg production [16–19]. The mate choice of females is mainly dependant on the males’ ability to offer nuptial gifts [20–22].

 The scorpionflies in the genus Panorpa are often treated as model animals for investigating mating systems of insects [23–27]. In general, to enhance male control and overcome female resistance in copulation, Panorpa males may offer females a dead arthropod or a salivary secretion as nuptial gift; or they may attempt a coercive mating without nuptial gifts [11,22,24]. Recent studies mainly focused on the function and evolution of nuptial feeding behaviours in scorpionflies [28–30]. The morphological basis of these behaviours, however, has not attracted sufficient attention.

 Various nuptial feeding behaviours are closely related to morphological specializations of the salivary glands of the male. Sexual dimorphism often occurs in the salivary glands of the Panorpa species whose male offers salivary secretion(s) to the female as a nuptial gift, the salivary glands being much more prominent in the male than in the female [16,31,32]. The well-developed salivary glands evidently provide the morphological basis for the males to secrete glandular masses as a nuptial gift. The structures of the male salivary glands, however, differ markedly both at generic and specific levels [33]. In Panorpa liui Hua the salivary glands are devoid of sexual dimorphism, only comprising two simple short secretory tubes in both sexes [34]. Accordingly, the male offers exclusively prey rather than salivary secretions as a nuptial gift to the female. On the other hand, the salivary glands of...
Neopanorpa also consist of only two simple elongate secretory tubes [33]. This renders us to explore the relationship of the mating behaviour and the morphology of Neopanorpa.

Neopanorpa Weele, the second largest genus in Panorpidae, occurs in the Oriental Region, especially abundant in the southern China and Southeast Asia [35]. Species of Neopanorpa are peculiar for their undeveloped salivary glands, developed notal organ, and distinctive male genitalia [33,36–39].

The notal organ is a clamp-like posterior process on tergum III in Panorpidae and is used to grasp the anterior edge of the female’s forewing during copulation [14,40,41]. This structure is regarded as an adaptation of Panorpa to enhance male control of copulation and to overcome female resistance [24]. It may enable males to prolong mating, especially conducive to coercive copulation and to overcome female resistance [24].

Genitalia play an important role in sexual interactions in insects [4]. Genitalic structures diverge rapidly over evolutionary time than general body features, often differing greatly among closely related taxa whose general structures differ only slightly [2–4,34,44]. Current knowledge on the genitalic structures of scorpionflies is mainly concentrated on their values in taxonomy and species delimitation. Their functional morphology has largely been ignored to date [40,45–53], although a preliminary investigation was conducted in P. julennis [34].

Here two questions arise: why the males of Neopanorpa have such an elongated notal organ? And what is the evolutionary significance of the notal organ? In this paper we investigated the mating behaviour and mechanism of Neopanorpa longiprocessa Hua & Chou, 1997 through observations of mating behaviour under laboratory conditions and of morphology using light microscopy and scanning electron microscopy.

Materials and Methods

Ethics Statement

No specific permits were required for the described field studies:

a) no specific permissions were required for these locations/ activities; b) locations were not privately-owned or protected; and c) the field studies did not involve endangered or protected species.

Insect Collection

Neopanorpa longiprocessa Hua & Chou is one of the northernmost species of the genus, extending as northward as to the Qinling Mountains of central China [37]. Adults were collected at the Huoditang Forest Farm (33°26’N, 108°26’E, elev. 1590–1830 m) in the Qinling Mountains, Ningshan County, Shaanxi Province, China from late May to August in 2010–2012.

Insect Rearing

The adults collected were transported to the laboratory in the Huoditang Forest Farm. The rearing method followed Thornhill and Sauer [14] and Engqvist and Sauer [55]. Throughout the experiment, adults were held in screen cages (60×60×80 cm) containing twigs and leaves of plants and moist absorbent cotton. Each cage contained 10 males and 10 females. All individuals were marked on forewings to facilitate identification. The scorpionflies were reared at temperatures of 20±5°C during day-time and 15±3°C during night-time. The relative humidity was 70±5% during day-time and 85±5% during night-time. All the adults were reared under natural photoperiod (L:D = 14 h:10 h). Individuals in the cage were provided with dead beetles (Anomala sp. and Potosia sp.) and cicada (Cryptotympana sp.) as food item. Each individual was supplied 1/2 dead insect per day.

Mating Behaviour

The mating behaviour was observed every 15 min for one pair of mates till the dawn of the next day (4:45–5:15 AM), or the termination of the copulation of all pairs.

The recorded items include the initiation and duration of the mate attraction, the beginning and ending times of the seizing behaviour, and the initiation and duration of copulation. The mating strategy of the male was also recorded.

To determine whether laboratory conditions affect the calling and copulatory behaviours, field observations were added as well.

Light and Scanning Electron Microscopy

For light microscopy, specimens were fixed in situ in Carnoy’s solution (100% ethanol: glacial acetic acid = 3:1, v/v) for 12 h before being preserved in 75% ethanol. The genitalia were dissected under a Nikon SMZ168 stereoscopic zoom microscope. Some specimens were macerated in cold 10% sodium hydroxide solution for 1–2 h, cleaned in an ultrasonic cleaner for 60 s, and observed under a Nikon SMZ1500 stereo zoom microscope. Photographs were taken with a digital camera attached to the microscope and further treated with the software QImaging Retiga-2000R Auto-Montage.

For scanning electron microscopy (SEM), the ethanol-preserved specimens were dried in a critical-point drier after dehydration in a graded ethanol series, coated with gold in a sputter coater, and examined in a Hitachi S-3400N scanning electron microscope (Hitachi, Tokyo, Japan) at 15 kV.

Results

Mating Behaviour

The mating behaviour of N. longiprocessa may occur anytime in a day except dawn under laboratory conditions. The mating process can be divided into three phases: calling (mate attraction), seizing, and copulating phases. In all the cases of observation, these phases occur without nuptial feeding. Neither dead insect nor salivary secretion was provided as a nuptial gift. No significant difference of mating behaviour was found between the laboratory and field conditions.

During the calling phase, the male attracts the female through odoriferous communication. The male stretches the hypandrium ventrally to expose the everted paired pouch-shaped pheromone glands in the genital bulb to emit sex pheromones that lure the females nearby, as in Panorpa [56–58]. Once the female responses to the attraction and approaches to the male, he terminates pheromone emission by reverting the pheromone glands. The everting and reverting of the pheromone glands marked the initiation and termination of the mate attraction. The male approaches the receptive female and pounces on her, curves his abdomen upwards while vibrating wings rapidly, and tries to overlap her wings with his wings. When the female is close enough, the male clamps her wings (usually the right side) with his notal organ, and enters into the seizing phase.

The seizing phase starts when the male holds the wings of the female with his notal organ. The seizing phase, the male keeps clamping the wings of the female. Then he stretches out his abdomen, and seizes the abdominal end (abdominal segments X and XI), especially the cerci of the female with his hypovalves (sometimes also with gonostyl). After that, the male attempts to pair his genitalia with hers. Usually the female struggles to get rid of the male. The seizing phase could be prolonged and even repeated. This phase can last for hours under laboratory conditions. The duration of the seizing phase is
121.17 ± 41.05 min on average for the 70 pairs of successful copulations.

Once the male has successfully seized the female, he usually attempts to adjust his position to connect their genitalia. The copulating phase starts when the male genital bulb completely encases the female abdominal segments IX–XI (Figures 1 and 2). During copulation, the male keeps clamping the wings of the female from one side with his notal organ (Figure 1) and on the distal abdominal segments with his genital bulb (Figure 2). The coupling pair maintains a V-shaped position (Figure 1).

Sometimes the female twists and/or withdraws her abdomen to try to terminate copulation. Although this resistance can interfere in the copulation, the female is hardly to get rid of the male from steady notal organ clamping. In general, the male will try to reseize the female terminalia with his genitalic clasping structures. The copulation continues after the male reseizes and repositions the female.

The copulating phase terminates when the male loosens his gonostyli and releases his grip on the female abdomen. The copulation duration is 145.64 ± 59.44 min in 70 pairs of successful copulations. Then the male releases the notal organ to free the wings of the female. The female struggles for seconds to disconnect her genitalia from the male's genital bulb, and then walks away.

Morphology of the Notal Organ

The natal organ of *N. longiprocessa* males is an extremely elongated posterior process on tergum III, extending to the half-way of tergum V, and is used to clamp the wings of the female together with the raised postnotal process on tergum IV during copulation (Figure 1). The ventral surface of the natal organ is

**Figure 1.** A pair of *Neopanorpa longiprocessa* in copula. The male (the left side) clamps the left wings of the female (the right side) with his notal organ.

**Figure 2.** Genitalia of *N. longiprocessa* in copula, with the female at the up and the male at the bottom. Ce, cercus; Gc, gonocoxite; Gs, gonostylus; Hv, hypovalve; Hy, hypandrium.

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densely furnished with pointed long setae, inversed and directed antero-ventrally (Figures 3A and B). The postnotal process of tergum IV is raised dorsad (Figure 3C), and is densely set with thick anterodorsad-directed setae (Figure 3D). The anterior half of tergum IV is weakly sclerotized, and sparsely covered with numerous microtrichia (Figure 3E).

The forewings of the female bear microtrichia on the upper surface and setae along the veins (Figures 3F). These setae interlace with the setae on the natal organ, and impede the female from escaping.

Genitalic Structures of the Male

Functionally, the male genitalic structures can be divided into interconnecting and grasping structures. The former (penis) is used to connect to the female genitalic during copulation. The latter (including gonostylus, epandrium, and hypandrium) is used to grasp particular part of the female during copulation.

The genital bulb of the male *N. longiprocessa* consists of the epandrium (tergum IX), hypandrium (sternum IX), and genitalia. The genitalia consist of paired lateral gonopods and the central valved penis (Figures 4 and 5). The gonopod is two-segmented, comprising the basal gonocoxite and the distal gonostylus (Figure 4).

The strongly sclerotized penis is composed of bilobed ventral and dorsal valves with the phallotrema situated centrally among the valves (Figures 5, 6A and B). The valved penis is not an intromittent organ and lacks endophallus anatomically (Figures 5, 6A and B).

The paired parameres are basally fused with the penis, consisting of a single basal stalk and paired distal branches (Figure 6A). The ventral branch can stretch ventrally for a limited angle (Figure 6B).

The elongated gonostyli are claspsers, grasping the female terminalia during copulation (Figures 1 and 2). Usually, the gonostylus steadily clamp the female’s segment IX at the base, press her body wall to open the genital chamber and to expose the genital plate, at the apex of which is situated the orifice of the spermathecal duct. Each gonostylus has a prominent basal process, which bears long setae, with the median part concaved (Figure 6C). These processes help deform the integument of the female’s genital chamber, impeding the genital plate from retreating (Figure 2).

The hypandrium consists of a broad basal stalk and a pair of slender distal hypovalves. The hypovalves are convex ventrally,

![Figure 3. The natal organ and postnotal process of the male and the wing surface of the female in *N. longiprocessa*. (A) Notal organ, lateral view. (B) Magnification of the natal organ in lateral view, showing the setae. (C) Postnotal process, laterodorsal view. (D) Magnification of the postnotal process, showing the setae. (E) Magnification of the dorsal surface of the anterior half of the 4th tergum. (F) Upper surface of the female forewing. doi:10.1371/journal.pone.0074781.g003](http://www.plosone.org/doi/10.1371/journal.pone.0074781.g003)
with their dorsal surface rough and bearing irregular micro-sculpturing (Figure 6E). Each hypovalve subbasally has a blunt dorsad-directing process, which bears numerous thick setae on the mesal surface (Figures 6D and E).

The epandrium bears subapically a pair of greatly expanded ventral bulbs, which are weakly sclerotized and produced posteriorly (Figures 5 and 6F). The paired bulbs fill the space between the epandrium and penis (Figure 5).

Genitalic Structures of the Female

The genitalia of the female are located on the abdominal segment IX, consisting of a subgenital plate and a genital plate (Figure 7A). The subgenital plate is emarginate distally in a V shape, implying its paired origin (Figure 7B), and curves dorsally from each side to form a shallow genital chamber, in which the genital plate is situated (Figure 6D and E).

The genital plate is a heavily sclerotized structure, consisting of the main plate and the axis. The main plate extends backward, forming paired posterior arms (Figure 7C). In the axis, the spermathecal duct is fixed in the midventral groove and the irregular-shaped copulatory pore is situated medially at the posterior end (Figure 7D). The genital plate can stretch out to connect her copulatory pore to the phallothrem of the male penis.

Discussion

To our knowledge, this research is the first attempt to explore the copulatory mechanism in Neopanorpa scorpionflies. N. longiprocessa is peculiar for the male to seize the female for a long period and not to provide edible nuptial gifts during mating. The developed notal organ of the male plays an important role in the seizing phase. Some specialized structures in the male genitalia, such as epandrial bulbs and hypandrial processes, may be used to counter against the female resistance.

Co-Evolution of the Mating Behaviour and Male Apparatuses

Male Panorpa scorpionflies may obtain mating in three alternative tactics: offering salivary masses, offering dead arthropods, or coercive copulation without nuptial gifts [15,24]. In Panorpa the females mate selectively with males that provide edible gifts, and discriminate against the males that fail to offer nutriments either by rejection or by copulation only for a short time [16,20–22]. Hence, the coercive copulation is considered as the most ineffective tactic because of the female resistance, which causes the shortening of copulation duration and the decreasing of the sperm transfer rate [16,59].

Coercive copulation is more unusual than the other two tactics in Panorpa [55,60]. In some North American and Japanese species of Panorpa, the males usually provide dead arthropods as nuptial gifts. However, the tactic of coercive copulation happens occasionally for the weak or less competitive males [13,15,61].

The peculiarity of the mating behaviour in N. longiprocessa lies on that the copulation has nothing to do with nuptial feeding. The males of N. longiprocessa use the developed notal organ to clamp the wings of the female. Only the male that succeeds in seizing the female can establish genital contact and copulate with her. The seizing phase in N. longiprocessa takes almost equal time to copulation. Since the male copulates coercively with the female, he must conquer the resistance from the female. In this case, the male genitalia could contact with the counterparts of the female and keep stability for sperm transfer. This mode of copulation may promote the morphological evolution of the male, and is likely one of the possible reasons for the copulatory apparatuses of N. longiprocessa to diverge rapidly from those of Panorpa scorpionflies.

Quite different from Panorpa scorpionflies with undeveloped notal organs in males [40,42], the developed notal organ can...
explain the coercive mating behaviour in *N. longiprocessa*. The notal organ of *N. longiprocessa* is extremely developed, almost corresponding to the width of female’s wings and bear dense setae, both of which likely impede the female wings from withdrawing.

The notal organ of male *Panorpa* scorpionflies is regarded as a modified appendage that can be used in coercive mating behaviours [13,15]. The function of notal organ was once considered to prolong copulation against female interests [14]. Recent studies, however, show that in some species the organ may not contribute to prolonging copulation [55,62]. On the other hand, the notal organ exhibits interspecific diversity in the genus *Panorpa* (cf. 34,40–42,54), which is likely one of the possible reasons for the difference in ability to prolong copulation.

On the basis of our unpublished comparative study, the developmental degree of the notal organ is negatively correlated with that of the male salivary glands, and vice versa. This phenomenon probably affects the evolution of mating strategy of the males. Males of *P. luir* are characterized by a developed notal organ and a simple undeveloped salivary gland [33,34,63], and are unable to generate salivary secretions. Thus the males provide only dead arthropods (prey) as nuptial gifts [34]. Males of the North American *P. nuptialis* and the Japanese *P. japonica* share morphological similarity of notal organ with *P. luir*. Likewise, they produce no salivary secretion for the female to feed upon [40,61,64]. The males of *Neopanorpa* usually bear a well-developed natal organ and undeveloped salivary gland [33,63]. Our result may partly explain the structural reason why the males of *N. longiprocessa* do not offer salivary secretion as their nuptial gift: males are too weak with respect to their salivary glands to produce enough saliva offered to females during copulation.

Conflict over control of copulation also drives the evolution of male genitalic structures [7,44,66]. The specialized genitalia enhance male ability to control over copulation [3,4]. In scorpionflies males have evolved specialized genitalia to take advantages in sexual conflict. Their functional morphology has been preliminarily explored in *P. jilinensis* [54]. However, the roles of genitalia in copulation have not been satisfactorily investigated in *Neopanorpa*.

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**Figure 6. Male genitalic structures of *N. longiprocessa*.** (A) Valved penis and parameres, ventral view. (B) Same, caudodorsal view, arrow showing the phalotreme. (C) Left gonostylus, ventral view. (D) Hypovalves, lateral view, arrow showing the hypandrial process. (E) Same, dorsal view, arrow showing the hypandrial process. (F) Apical part of the epandrium in ventral view, showing the epandrial bulb. BP, basal process; Ce, cercus; DV, dorsal valve of penis; EpB, epandrial bulb; Pm, paramere; VV, ventral valve of penis.

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The specialized gonostylus, epandrium, and hypandrium of the male of *N. longiprocessa* are used to grasp particular part of the female abdomen. The gonopods are called as genital claspers [67], indicating their function as claspers to clamp the female during mating. The movable gonostyli, to be more precise, are particularly used as “claspers”. Long setae on the basal process are likely used to increase friction during the seizing phase.

The structure of the male hypovalves in *Neopanorpa* is characterized by the paired hypandrial processes [36,38]. The modification of this structure leads to the changes of the functions of hypovalves in the courtship and copulation of *N. longiprocessa*. In the seizing period, the male of *N. longiprocessa* uses his hypovalves to entangle the female stretched terminalia and infibulate her cerci. It allows the male to restrict the movement of the female abdomen and easily to approach the female genitalia at the following interactions. During copulation the hypovalves are used to entrap the female’s terminalia not to move till the male releases the female. We speculate that the irregular microsculpturing on the dorsal surface of the hypovalves is likely used to increase friction between the hypovalves and the counterpart of the female.

The epandrial bulb is another specialized genital structure in *N. longiprocessa*. According to Miyaké [45], who illustrated the copulatory posture of external genitalia of both sexes in *Panorpa klugi*, we speculate that the epandrial bulb in *N. longiprocessa* likely serves to entrap female’s subgenital plate between the ventral surface of the epandrium and the dorsal surface of the gonocoxites by a specialized genital structure. The moveable apical part of the epandrium could firmly fasten the female terminalia, allowing the male penis to connect with the orifice of the spermathecal duct in the female genital chamber during copulation.

Morphological modification in genitalia and other contact structures is a widespread strategy in male insects to adapt to overcome the female resistance over copulation in sexual conflict [4,7]. Male strategies aimed at succeeding in copulation can increase mating costs of the female through sexual conflict [9,68]. The costs, including energetic cost, injury, disease, and predation risk, may cause decrease of female fitness [8,69]. Thus, the females primarily attempt to decrease or avoid male-imposed mating costs rather than acquire benefits from males [8,70]. In *N. longiprocessa*, to conquer the female resistance, the male has evolved an extremely elongated notal organ and specialized genitalia, which are used to seize the female during mating. The seized female usually struggles to escape, likely increasing the mating costs through energetic consumption. Due to the increasing mating costs during struggle, the female is likely to yield and accept the copulation. Thus, the non-nuptial feeding mating of *N. longiprocessa* is likely evolved through sexual conflict in scorpionflies. These structural adaptations in *N. longiprocessa* may represent another evolutionary pathway different from *Panorpa* to overcome female resistance.

**Copulatory Mechanism**

In general, the male of pterygote insects insert his aedeagus (endophallus) into the reproductive tract of the female during insemination [6]. The male *N. longiprocessa*, however, possesses a valve penis and lacks a median intromittent organ. The male connects his phallostrem to the female copulatory pore for sperm transfer, as in *P. jilinensis* [54]. Thus the female is easy to disconnect with the male during copulation. Accordingly, it is the male’s interest to evolve specialized structures to overcome the female resistance and complete the copulation in *Neopanorpa*.

The copulatory mechanism in Panorpidae has only been studied in some species, such as *P. jilinensis* [54], although Miyaké illustrated the function of particular genital structures in *Panorpa klugi* [45]. On the basis of the behavioral observations and the ultrastructure of the external genitalia, we suggest that copulatory mechanism of *N. longiprocessa* is as follows. Having seized the female with his notal organ, the male adjusts his

![Figure 7. Female genitalia of *N. longiprocessa*. (A) Abdominal segments VIII–XI, lateral view. (B) Abdominal segments IX–XI, ventral view. (C) Genital plate, ventral view. (D) Same, caudal view, arrow showing the copulatory pore (orifice of the spermathecal duct). Ax, axis; Ce, cercus; CP, copulatory pore; PA, posterior arm; SP, subgenital plate.](figure.png)
genital position to allow the phallothrema to connect to the copulatory pore (the orifice of the spermathecal duct) of the female to allow the phallotreme to connect to the female subgenital plate, and finally uses its hypovalves to clip the female cerci. These genital structures of the male restrict the movements of the female, allowing the male to hold the female genitalia tightly against the resistance (Figure 2).

Elucidating copulatory mechanism may help understand the sexual conflict in scorpionflies. In this study, however, detailed genital contacts during copulation have not been worked out between the male and female genitalia. The precise copulatory mechanism awaits additional studies using freeze-fixation of copulating pairs, as exemplified by Eberhard & Ramirez [71].

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Author Contributions

Conceived and designed the experiments: BZH WZ. Performed the experiments: WZ. Analyzed the data: WZ. Wrote the paper: WZ BZH.
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