

M. Thiel

Reproductive biology of a small isopod symbiont living on a large isopod host: from the maternal marsupium to the protective grip of guarding males

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Abstract Mating systems of many symbiotic crustaceans are characterised by a high degree of mate guarding. A peculiar case of mate guarding has been reported for small symbiotic janirid isopods where males mate with immature females. Field samples of individual hosts and laboratory experiments were conducted to reveal the mating behaviour of the symbiont in a natural environment, that is, on their hosts. Along the coast of the Magellan Strait, Chile, the janirid isopod *Iais pubescens* was frequently found on the shore-living isopod *Exosphaeroma gigas*. Symbiont prevalence (percent hosts occupied) was high at eight of the nine sampling sites. Mean symbiont intensity was very low at one site ($<< 1$ individual host⁻¹), intermediate at two sites (1–10 individuals host⁻¹) and high at the other sites (10–40 individuals host⁻¹). The mean sex ratio (males:females) was male biased at most sampling sites ($n=7$). Females of *I. pubescens* reached substantially larger sizes (1.5–3.0 mm body length, BL) than males (1.1–1.9 mm BL). The majority of males were carrying small juveniles (66.15%), and males with juveniles were significantly larger than males without juveniles – this suggests that males prefer virgin juveniles to adult females and that they compete for small juveniles. In laboratory observations, males were seen to manipulate the marsupium of adult females that were about to release small juveniles. Males obtained virgin juveniles in this manner. Juveniles were carried for ~7 days, and they moulted shortly before being fertilised and released by males. The high proportion of juveniles carried by males in the field (68.2%) supports previous observations that males initially are not able to distinguish male and female juveniles. It is suggested that the mating system of symbiotic

janirid isopods with long-term sperm storage and continuous receptivity in females and male mating with virgin females has evolved in response to highly unpredictable encounter probabilities between the sexes. Mate guarding and manipulation of small virgin juveniles may be favoured on the highly mobile hosts of symbiotic janirid isopods. Furthermore, adult females may gain by leaving their emerging offspring in the protective grip of guarding males, thereby reinforcing the maintenance of this peculiar mating system.

Introduction

The mating systems of crustaceans are highly diverse, ranging from promiscuity over harem-like groups to highly monogamous pairs (Wirtz and Diesel 1983; Christy 1987; Bauer 1996; Johnson et al. 2001). In the majority of species it is the males that search for or monopolise females. Males may attempt to mate with any receptive female they encounter or they may guard one or several females for prolonged periods of time awaiting their reproductive moult. Mating systems of symbiotic crustaceans are similarly diverse as those of free-living crustaceans, but they are characterised by a high degree of specific association patterns of mating partners on hosts. In particular the size and availability of hosts may impose restrictions on the mating behaviour of symbiotic crustaceans (e.g. Thiel and Baeza 2001). Leaving hosts in search of mating partners may represent a high risk for the searching sex. Similarly the ability to monopolise a large host to which mating partners can be attracted might affect the mating success of individuals. These restrictions may have resulted in the evolution of highly complex mating systems in symbiotic crustaceans.

One peculiar mating system is found in small symbiotic isopods from the family Janiridae. In these species, males mate with immature females, which store sperm until reaching sexual maturity (Franke 1993).

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M. Thiel
Facultad Ciencias del Mar,
Universidad Católica del Norte,
Larrondo 1281, Coquimbo, Chile
E-mail: thiel@ucn.cl

Mating of males with immature females has also been reported for some free-living janirids (Kensley 1994), but it appears to be a typical behaviour in symbiotic janirids. Interestingly, males of most free-living janirid isopods mate with adult females shortly after the reproductive moult of females, similar to the system reported for most other crustaceans. This suggests that the peculiar mating system of symbiotic janirids has evolved in response to factors related to their symbiotic lifestyle. The hosts of these small isopods (~ 2 mm body length, BL) are comparatively large (~ 20 mm BL) and highly mobile, suggesting that hosts cannot be efficiently monopolised as is the case in many other symbiotic crustacean species.

The symbiotic janirid isopods live on the ventral surface of sphaeromatid isopods (Rotramel 1975; Prunus and Pantoustier 1977; Marsden 1982; Franke 1993). Adult males of most symbiotic janirid species are smaller than adult females and mate with immature manca-I females (Franke 1993). Males can also mate with large females but they appear to prefer small manca-I despite the high costs associated with this behaviour: males carry manca-I for long time periods (8–10 days) and they are incapable of distinguishing male from female manca-I (Franke 1993). This preference for manca-I was revealed for the symbiotic janirid, *Jaera hopeana*, but in a host-less environment (Franke 1993). In nature, various symbiont individuals may share the same host individual, and aggregations of more than 25 individuals on a single host individual have been reported (Marsden 1982). Most commonly, however, the number of symbionts on one host individual appears to vary around 10 individuals host⁻¹ (Marsden 1982). Encounter probabilities, to which males and females are

exposed in host-less experiments, may not be representative of a natural situation, that is, when living on their hosts. Presently it is not known how males obtain their immature mating partners and how long they guard them in a natural situation. This knowledge is considered essential to understanding the evolution of the mating system of symbiotic janirid isopods.

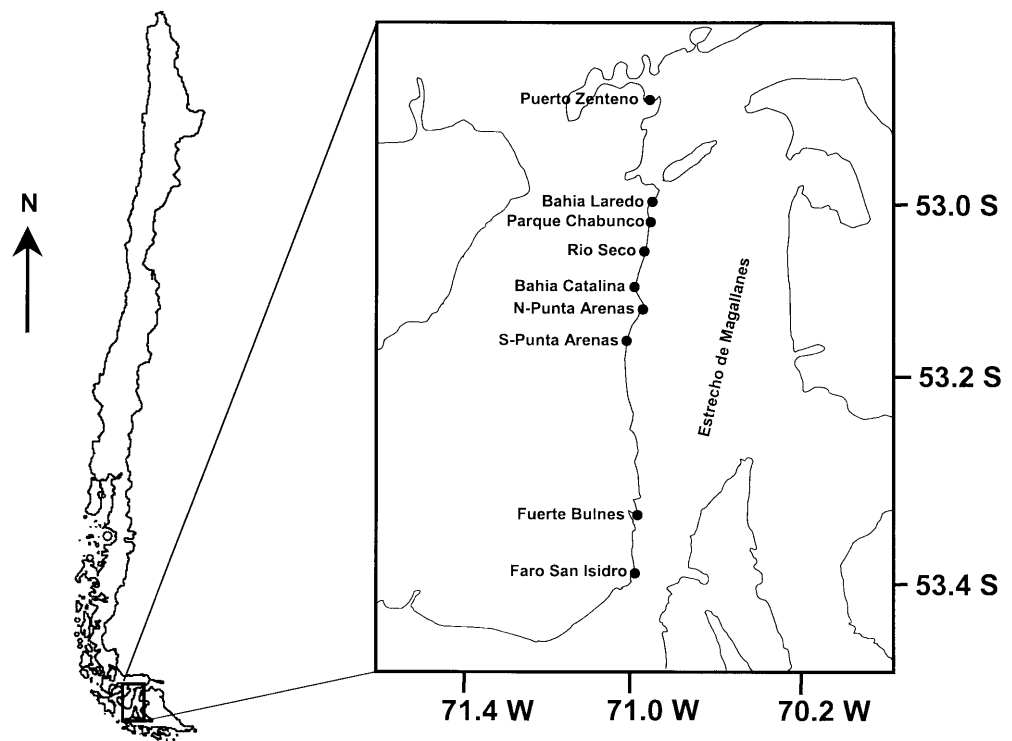
The main objective of this study was to reveal the mating behaviour of a symbiotic janirid isopod in a natural environment. Field samples were taken to reveal what percentage and sizes of small juveniles are carried by males under natural conditions, that is, while on their hosts. Furthermore, I conducted laboratory observations and experiments in which symbionts were maintained on their natural hosts, to reveal how males obtain their mates and how long they carry them in a natural environment.

Materials and methods

Study site

Field samples were taken in March 2000 in the intertidal zone along the Chilean coast of the Magellan Strait (Fig. 1). The shores in this region are characterised by an abundance of boulders of varying sizes (diameters 0.1 to > 1 m), and gravel of smaller grain size. The mobile fauna associated with these boulder shores comprises mainly polychaetes, crustaceans, and gastropods (Mutschke et al. 1998). Sphaeromatid isopods *Exosphaeroma gigas*, which are important hosts of the small janirid isopod *Iais pubescens*, occur in dense aggregations of several hundred individuals underneath boulders. At each of nine sampling sites, approximately 25 individuals ($n=25-29$) of *E. gigas* were collected and immediately isolated in small vials.

Fig. 1. Map of the study area in the Magellan Strait (*Estrecho de Magallanes*) near Punta Arenas, Chile with the nine sampling sites



Processing and measurements of *I. pubescens*

All host isopods were preserved in 4% Formalin for later measurements and examination of the janirid symbionts. In the laboratory, each host individual was carefully surveyed for symbionts with the aid of a dissecting microscope. After removing all symbionts, the host individuals (*E. gigas*) as well as the symbionts (*I. pubescens*) were sexed and their sizes measured with the aid of a measurement ocular. Seven different life stages of *I. pubescens* individuals were distinguished (Table 1). Most juveniles ≤ 0.8 mm BL were in the manca-I stage. The smallest individuals in which penis appendages were recognisable slightly exceeded 1.0 mm BL. The smallest females that were found carrying embryos were > 1.6 mm BL, but in females > 1.5 mm BL the maturing gonads were often visible.

Behavioural observations of *I. pubescens*

Isopods for laboratory experiments and observations were collected at two sites (Parque Chabunco and Rio Seco). Observations of the behaviour of *I. pubescens* were conducted in the laboratory under a dissecting microscope. Hosts together with their symbionts were placed with their ventral side facing upwards in small jars that were filled with seawater from their natural environment. Symbionts were usually observed on their original host. In some cases, specific aggregations were artificially constructed. Females that were close to releasing their offspring from the marsupium were placed together with single males. Since living isopods were too small and too agile to examine for the presence of male appendages, males that were carrying small juveniles were separated from their respective juveniles. Following removal of juveniles, males

behaved apparently normally and immediately grabbed their juveniles again, if these were provided. Solitary males, to which juveniles were not returned, were placed on a host with a female ready to release offspring from the marsupium. Isopods were observed for several hours and their behaviour during these observations was recorded.

Experiment on duration of juvenile carrying by male *I. pubescens*

Isopods for this experiment were collected at two different sites (Parque Chabunco and Rio Seco). Symbionts were sorted from *E. gigas* collected at Parque Chabunco and later placed on *E. gigas* from Rio Seco, which were naturally almost free of symbionts. Ten male *I. pubescens* that were already carrying juveniles were placed on one host individual from Rio Seco. Before symbionts were placed on the host's body, each host was carefully examined to ensure that it indeed did not carry any *I. pubescens*. One host individual together with the ten juvenile-carrying males was placed in a small vial filled with seawater (40 ml). Twenty replicate hosts were equipped with symbionts in this manner. Fresh seawater was collected each day from the natural habitat of the isopods, and water in the vials was exchanged every day. All isopods used in this experiment were collected in the field during the morning low tide and immediately transferred to the laboratory where they were sorted during the day. The experiment was then started in the late afternoon and water was changed every afternoon throughout the following days.

The first three host individuals with their symbionts were sampled 2 days after the experiment was set up. Thereafter each day three hosts were sampled, with the exception of day 8, when only two hosts remained. The hosts were fixed in 4% Formalin and later examined for their symbionts. Preliminary laboratory observations had revealed that male *I. pubescens* firmly held on to "their" juveniles during the fixation process. This allowed the distinction of juveniles that had already been liberated and juveniles that were still carried by males on the respective days. After having been sorted, all male and juvenile symbionts were measured.

Table 1. Life stages of *Iais pubescens* and morphological and behavioural criteria that were used to distinguish them

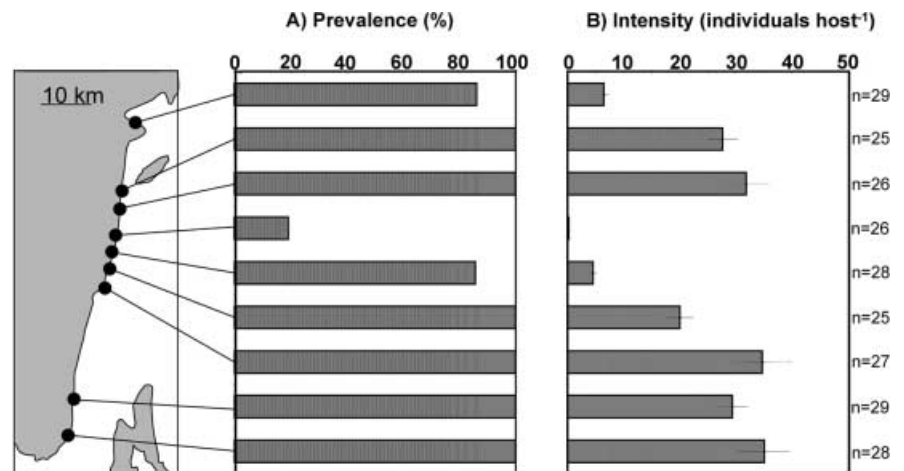
Life stage	Criterion
Juvenile, single	≤ 0.8 mm, not carried by male
Juvenile, carried	≤ 0.8 mm, carried by male
Sub-adult	> 0.8 mm to ≤ 1.5 mm, without male appendages or marsupium
Male, single	> 1.1 mm, male appendages, without juvenile
Male, carrying	> 1.1 mm, male appendages, carrying juvenile
Female, non-reproductive	> 1.5 mm, often gonads with oocytes visible
Female, reproductive	> 1.5 mm, with marsupium, ovigerous

Results

Population structure of *Iais pubescens*

At most sites, almost all isopods *Exosphaeroma gigas* hosted the symbiont *I. pubescens* (Fig. 2A) with the exception of one site (Rio Seco), where only a few sphaeromatids were found with the symbionts. The density of *I. pubescens* on single host individuals was low at three

Fig. 2A, B. *Iais pubescens*. **A** Prevalence (percentage of hosts with symbionts) and **B** intensity (symbionts per host individual) of symbiotic isopods on their host, the sphaeromatid isopod *Exosphaeroma gigas*, at the nine sampling sites in Estrecho de Magallanes near Punta Arenas, Chile; *n* = number of hosts collected at each site



sites and reached average values of ~ 30 symbionts host⁻¹ at most of the other sites (Fig. 2B). The maximum number of symbionts found on one host individual was 125 *I. pubescens* on one *E. gigas* from S-Punta Arenas. Female *I. pubescens* were substantially larger than males (Fig. 3A). The majority of females had sizes ranging from 1.5 to 2.5 mm BL, but one female (non-ovigerous) had a BL of 3.1 mm. Male body sizes ranged from 1.1 to 1.9 mm BL, and the majority of juveniles and sub-adults were <1.0 mm BL (Fig. 3B, C). The sex ratio (males: females) at the nine sampling sites varied between 0.63 and 2.72, being male-biased at most sites ($n=7$).

Juveniles carried by males were slightly larger than the last stages that were found in the marsupium of the females (Fig. 4A, B). Of the small juveniles (≤ 0.8 mm BL) collected during this study ($n=1,367$), 23.0% were free on the hosts, 68.2% were carried by males, and 8.8% were found in the marsupia of females (Fig. 4). The proportion of small juveniles carried by males was significantly larger than that of juveniles found in the females' marsupia or free on their hosts (χ^2 test of independence with Yates correction, $\chi^2=1220.6$, $df=2$, $P<<0.05$). This indicates that shortly after reaching the manca-I stage in the marsupium, juveniles emerge from the marsupium and thereafter are carried by males. Similarly, shortly after being released again by males, juveniles apparently grow to the next stage, since a relatively low proportion of small juveniles were found

living free on hosts. During the entire study only nine small sub-adults (all were >0.8 mm and ≤ 0.9 mm BL) were found being carried by males – all of these individuals were in the process of moulting, as indicated by the fact that they had shed the posterior part of their exoskeleton.

The majority of male *I. pubescens* were carrying small juveniles. Of all males collected ($n=1,418$), 66.15% were carrying juveniles and 33.85% were without juveniles. Among the small males (<1.4 mm BL) a relatively large percentage were without juveniles (Fig. 5A) compared to intermediate (1.4–1.6 mm BL) and large males (>1.6 mm BL) (Fig. 5B). Males with juveniles were significantly larger than males without juveniles (t -test, $t_{2,1416}=11.503$, $P<<0.01$). This may indicate that competition for small juveniles exists among males, and that larger males are favoured in obtaining and guarding juveniles. When comparing the relationship between symbiont intensity (symbionts per host) and the proportion of males carrying juveniles at the nine sites, a significant positive relationship was found (Fig. 6A): with increasing population density a higher proportion of male *I. pubescens* were carrying juveniles. At all sites where symbiont intensity was >5 symbionts host⁻¹, more than 50% of the males were carrying juveniles. A similar relationship between symbiont intensity and the percentage of reproductive females was found (Fig. 6B):

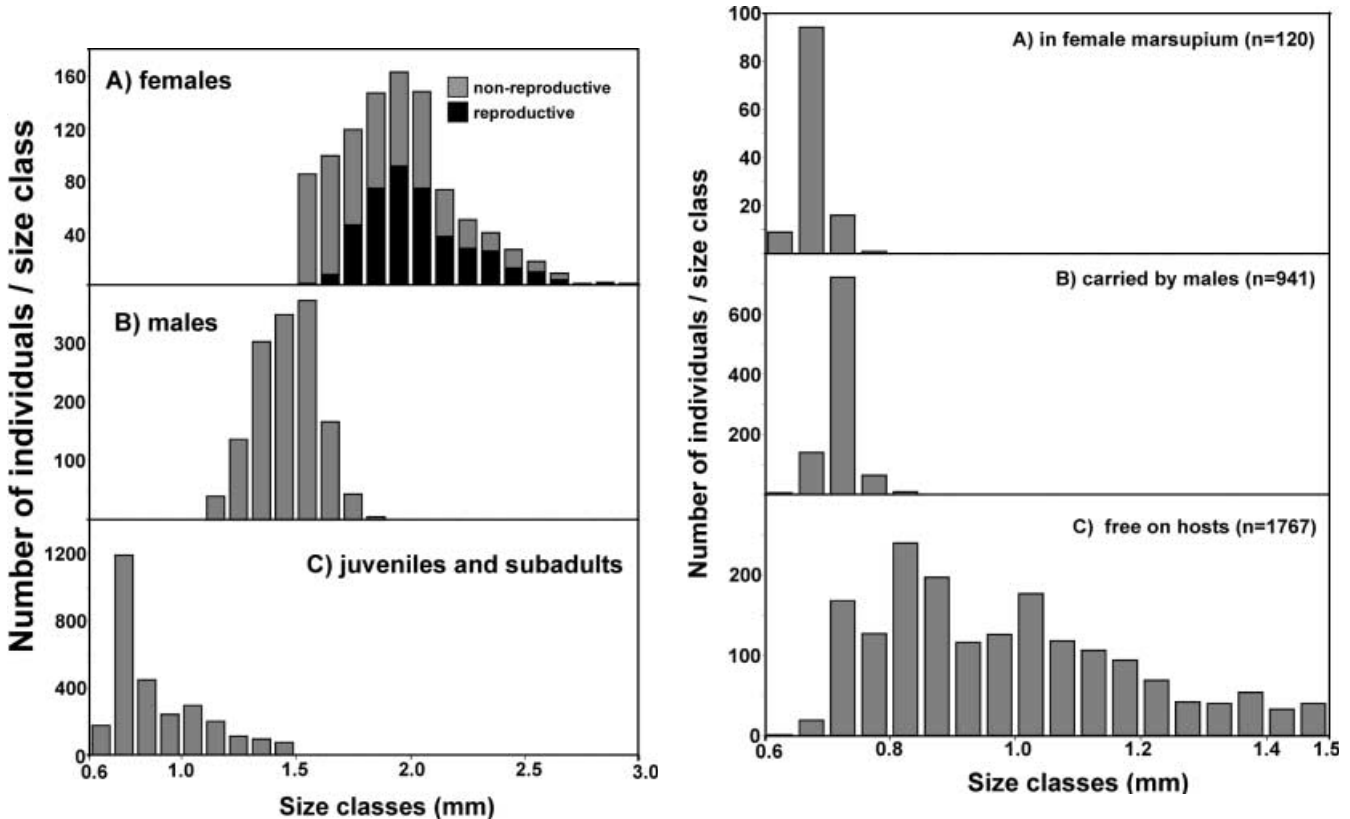


Fig. 3A–C. *I. pubescens*. Number of **A** females, **B** males, and **C** juveniles and sub-adults in respective size classes; symbiotic isopods from all sampling sites were pooled

Fig. 4A–C. *I. pubescens*. Number of juveniles and sub-adults in the respective size classes found **A** in the marsupium of their mother, **B** carried by males, or **C** free on their hosts; symbiotic isopods from all sites were pooled

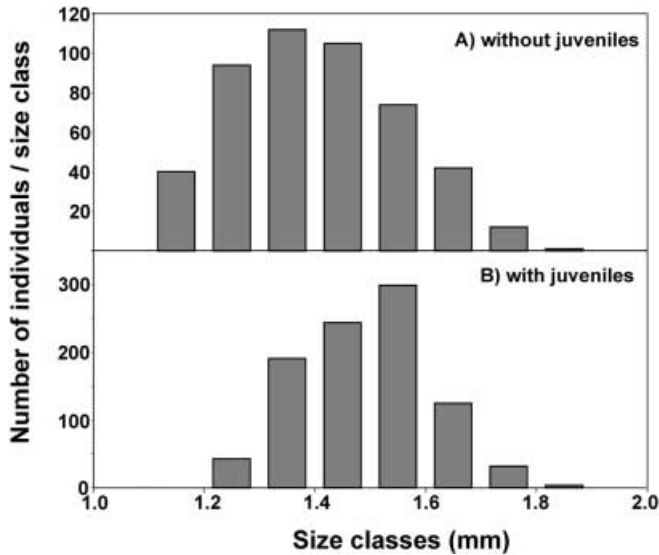


Fig. 5A, B. *I. pubescens*. Number of males in the respective size classes that were found as **A** singles or **B** carrying juveniles; symbiotic isopods from all sites were pooled

at high symbiont intensities, ~50% of the females were reproductive, but at low symbiont intensities a large proportion of females were non-reproductive.

Laboratory observations of the behaviour of *I. pubescens*

The symbionts moved freely over the ventral side and the pereopods of their hosts. *Iais pubescens* was frequently observed to graze over the surface of its host. When symbionts occurred in dense aggregations on their hosts, frequent encounters between individuals were observed. When two *I. pubescens* met, they touched each other briefly (a few seconds) with their antennae and then continued with their original activity. Encounters between males and small juveniles occasionally lasted slightly longer (tens of seconds), and males examined the juveniles from all sides and eventually took them into a grip with their fourth pereopods. Juveniles that were carried by males were able to graze over the surface of their hosts without any apparent impediments (Fig. 7A).

Non-carrying males of *I. pubescens* that were placed together with a female that was about to release its offspring from the marsupium continued with their regular activities. However, upon antennal contact with the female their behaviour changed. Some of these males remained with the female and occasionally also climbed onto her back. Males attempted to reach to the ventral side of the female either from her back or by reaching underneath her head (Fig. 7B). They repeatedly manipulated the marsupium of the female without any apparent intervention by the female. On several occasions, a male was observed to “grab” a small juvenile (in the manca-I stage) out of the female’s marsupium. Following procurement of a juvenile in this way, the males

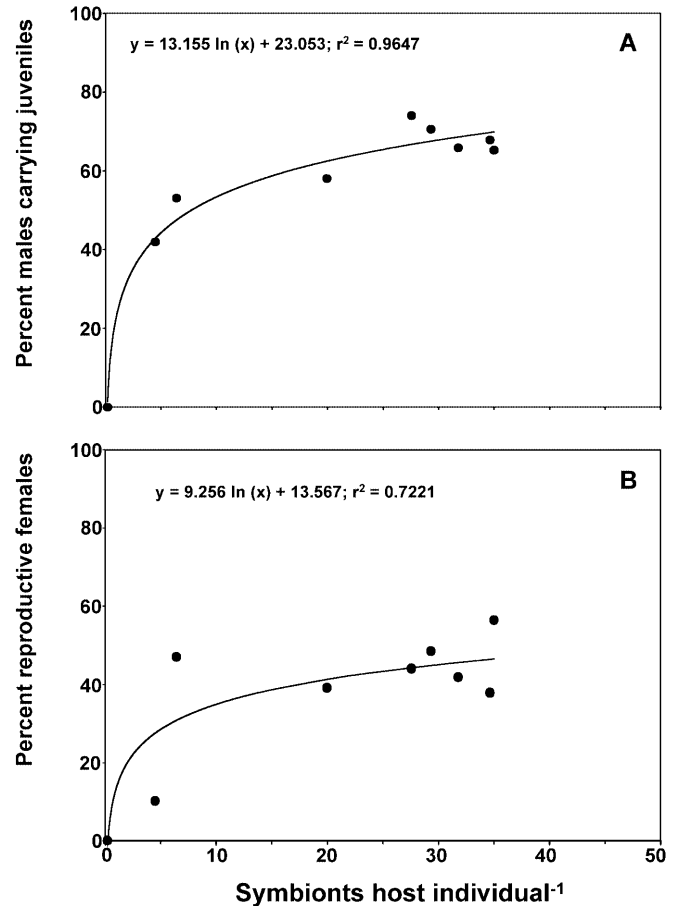


Fig. 6A, B. *I. pubescens*. **A** Percentage of males carrying juveniles and **B** percentage of reproductive females (ovigerous or with oostegites) in relation to average intensity (symbionts per host) at the nine sampling sites

apparently lost interest in the adult female, walked away a short distance, and started to examine the juvenile from all sides. After examining the newly obtained juvenile for a while (tens of seconds), males either walked away with it holding it with their fourth pereopods, or they left the juvenile behind, returning to the adult female. Juveniles that were left alone were subsequently examined by other passing males and eventually were carried away by another male. Several hours after starting to release juveniles from the marsupium females had released all their offspring – at this point all males were carrying juveniles.

Duration of juvenile carrying by male *I. pubescens* on their hosts

Juvenile-carrying males that were collected in the field and immediately isolated on individual hosts released juveniles over a time period of 7 days (Fig. 8A). At day 8 all males had released their juveniles. Since many males may have already been carrying juveniles for several days at the beginning of the experiment, only the last

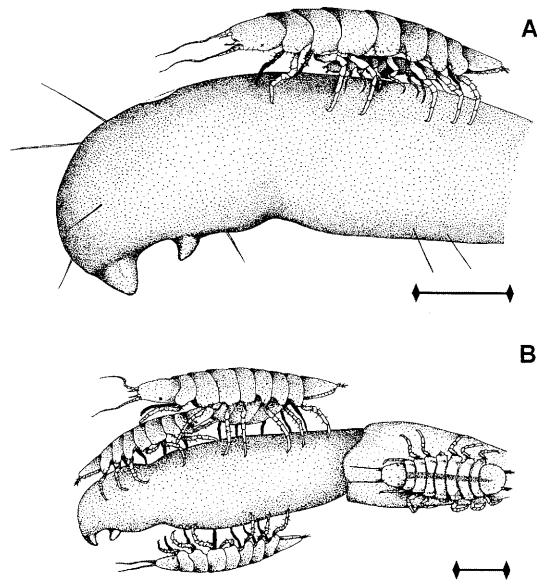


Fig. 7A, B. *I. pubescens*. A Male carrying juvenile in the typical carrying position; B several males surrounding an ovigerous female with juveniles ready to leave the marsupium, one male manipulating juveniles in the female's marsupium; scale bar 0.5 mm

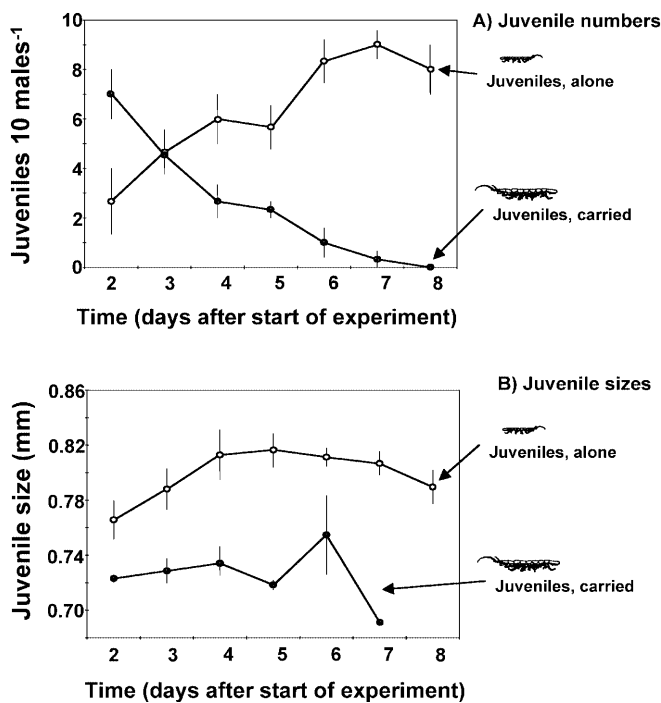


Fig. 8A, B. *I. pubescens*. A Average numbers and B average sizes of juveniles that were found as singles or still being carried by male conspecifics. At the beginning of the experiment ten males that were carrying juveniles were placed on one host individual *E. gigas*; experiment was started with 20 replicate hosts that were maintained in separate vials; each day 3 hosts with all their symbionts were sampled, with the exception of day 8 when only the 2 remaining hosts were sampled

males carrying juveniles should be considered to estimate the duration of juvenile carrying by males. Based on these considerations it can be concluded that male

I. pubescens carry juveniles for ~ 7 days. Juveniles that were found free on the hosts (after having been released by males) were 0.05–0.10 mm larger than juveniles that were carried by males (Fig. 8B), indicating that juveniles were released by males during or shortly after the first juvenile moult.

Discussion

The mating system of symbiotic janirid isopods

Males of the symbiotic isopod *Iais pubescens* carry small juveniles, which they obtain directly from the female's marsupium, for prolonged periods of time. On their natural hosts, males carried small juveniles for ~ 7 days, and the high percentage of small juveniles being carried indicates that males are not able to distinguish between male and female juveniles – these results confirm those previously obtained in laboratory experiments, in which symbionts were maintained without their hosts (Franke 1993). The results from the field samples indicate reduced reproductive activity at low symbiont intensities, possibly caused by low probabilities of male–female encounters. In contrast to most free-living janirid isopods, in which males mate with adult females, males of most symbiotic janirids are smaller than adult females. The mating system of symbiotic janirid isopods differs from that of most free-living janirids (and most other crustaceans) in two main aspects: (1) females present long-term sperm storage and continuous receptivity, and (2) males mate with small (virgin) females (Franke 1993). These mating adaptations of female and male janirids most likely have evolved in two separate steps as will be discussed below. Depending on the temporal order in which these evolutionary steps have occurred, two different scenarios can be envisioned.

Evolution of the mating system of symbiotic janirid isopods

The unpredictable sex-encounter scenario

Encounter probabilities between the sexes have strong effects on the evolution of mating systems (Emlen and Oring 1977). In addition to being affected by other factors, the probability of male–female encounters depends on the population densities of an organism. At low densities, the probability of male–female encounters will strongly diminish, and if females are only receptive during a short period of time (e.g. shortly after the receptive moult), they may face the risk of not being attended by a male at this moment. It may be under these circumstances that females evolve to become receptive throughout any phase of their reproductive life. Continuous female receptivity has been observed in the symbiotic janirid *Jaera hopeana* (Franke 1993), but also in the free-living janirid species *J. albifrons*. Adult

females of *J. albifrons* (free-living) and of *J. hopeana* (symbiotic) can store sperm (see Veuille 1980 and Franke 1993, respectively) to fertilise several subsequent broods. Long-lasting sperm storage does not occur in other free-living janirids – in these species females have to re-mate at the beginning of each sexual cycle (immediately after the reproductive moult). Possibly long-term storage of sperm (as found in *J. albifrons* and in *J. hopeana*) has evolved as a consequence of highly unpredictable male–female encounters during the reproductive moult of females. Veuille (1980) discusses the finding that large overwintering females of *J. albifrons* produce the first broods at the end of the winter, when population densities are low (Sjöberg 1970; Pantoustier and Prunus 1977). Also in symbiotic janirids, male–female encounters may be unpredictable at the end of the winter (Marsden 1982) or under other circumstances (e.g. low host abundance). The results shown herein indicate that at symbiont intensities of < 5 individuals host^{-1} reproductive activity of *I. pubescens* strongly diminishes (Fig. 6), most likely caused by low encounter rates between the sexes. Thus, continuous receptivity and long-term sperm storage in females may have evolved in response to low encounter probabilities between the sexes.

Symbiotic janirids also frequently occur in high densities (see, for example, Fig. 2). Under these conditions, the probability of male–female encounters strongly increases, enhancing the risk of sperm competition among males. In such a situation, males may engage in behaviours that reduce this risk, such as guarding receptive females. Given long-term sperm storage and continuous female receptivity in symbiotic janirids, even prolonged guarding of large females may not lead to a substantial reduction in the risk of sperm competition (see also Zimmer 2001). Furthermore, a study by Johnson (1982) indicates that in isopods, first males' sperm have a fertilisation advantage. This may force males to seek females that have not yet been in contact with other males, resulting in male preference for virgin females (see also Johnson 1982). In symbiotic janirids, the risk of sperm competition associated with large females may normally be so high that males guard small (virgin) juveniles even though they cannot distinguish juvenile females from juvenile males (Franke 1993; see above). Males may even compete actively for small virgin juveniles as is suggested by the fact that large males were more likely to carry juveniles than small males (Fig. 5).

The manipulation problem scenario

In most crustacean species, males actively manipulate the female before or during the mating process (e.g. Berg and Sandifer 1984; Aoki 1996). Guarding or manipulation of females may involve sophisticated behaviours, in particular when females are large or otherwise difficult to handle. Males may incur substantial costs during

guarding, and it is not unusual to find that males lose hold of the female during male–female struggles (Jormalainen 1998; Sparkes et al. 2000 and citations therein). On mobile hosts such as sea urchins or sphaeromatid isopods, prolonged guarding of large females may also be difficult. Such difficulties may cause males to engage in mating tactics other than guarding, for example those that can be characterised as “pure search and interception” (sensu Christy 1987): ‘Males wander around in search of receptive females and mating success appears to depend largely on differences in search efficiency’ (see also Bauer and Abdalla 2001). Instead of traits that favour guarding (size, fighting structures), morphological and behavioural traits that improve a male's efficiency in searching for females (small size, mobility) will be selected for. Consequently, adult males may be of the same size or even smaller than adult females (see also Christy 1987). Indeed, males of several crustacean species that live on complex and agile hosts are smaller (or at least not larger) than females (e.g. *Gnathophylloides mineri* – Patton et al. 1985; *Colidotia rostrata* – Stebbins 1988, 1989; *Athanas indicus* – Gherardi 1991). While manipulation problems could thus explain why males of symbiotic janirids do not engage in guarding of large females, such problems do not explain why they mate with small (virgin) females. Furthermore, to my present knowledge, in none of the other symbiotic species do females present long-term sperm storage and continuous receptivity.

In summary, the mating system of symbiotic janirid isopods most likely has evolved in consequence of the unpredictability of male–female encounters rather than of male problems in manipulating large females on their highly mobile hosts. The fact that mating (and guarding) of small juveniles is not restricted to symbiotic janirids (see Kensley 1994) indicates that conditions unrelated to a symbiotic lifestyle may have led to the evolution of this mating system.

Two additional factors may help maintain this peculiar mating system that is characterised by long-term sperm storage and continuous receptivity in females and male mating with small virgin females. Although the manipulation problem may not have been causative for the evolution of this mating system, it may nevertheless aid in its maintenance. On the highly mobile hosts of symbiotic janirids, small virgin females may convey an important advantage to the relatively small males: they may be efficiently hidden from other males and furthermore can be easily manipulated by the males (Hessler and Strömberg 1989). In addition, adult females and small juveniles may also benefit from the preference of males for virgin juveniles. Small juveniles that have recently emerged from the female's marsupium may be susceptible to sudden movements of their large isopod hosts. Since males apparently cannot distinguish the sex of small virgin juveniles, both male and female juveniles may improve their survival chances in the protective grip of mate-guarding males. This may also explain why adult females behave apparently indifferently towards

males grabbing small juveniles out of their marsupia. Adult females, by leaving their emerging offspring rather voluntarily to approaching males, may thus actively contribute to the maintenance of the peculiar mating system of symbiotic janirids.

Conclusions

Continuous receptivity and sperm storage by females as found in symbiotic janirid isopods may also evolve under other circumstances that prohibit frequent male–female encounters, such as, for example, in situations with high predation risk (Caldwell 1991; Henmi and Murai 1999). Under these conditions, mating partners show little choosiness – they mate with any member of the opposite sex that they encounter. With increasing probability of male–female encounters (e.g. at high population densities), mating partners become more choosy about their mates (see also Jennions and Petrie 1997). As has also been shown in studies on fish (Jirotkul 1999), crickets (Cade and Cade 1992), and mammals (Judge and de Waal 1997) under different population densities, males are exposed to different levels of competition and consequently may adapt their mating behaviour. Male *I. pubescens* may similarly adapt their mating behaviour (either mating with virgin juveniles or with mature females) in response to different population densities: at high population densities they mate with small virgin females and at low population densities they mate rapidly (“en passant” – sensu Franke 1993) with adult females.

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