Chapter 7
Male and Female Mate Choice in Harvestmen: General Patterns and Inferences on the Underlying Processes

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Abstract Harvestmen belong to the order Opiliones, and, unlike other arachnids, they are highly polygynandrous, with both males and females mating multiply throughout the breeding season. In this chapter, we review the current information on sexual selection in the group, focusing mostly on intersexual interactions. Particularly, we provide an overview of harvestman mating systems, examine different temporal phases of male–female sexual interactions, and explore cases of sex role reversal. Several traits in harvestmen make them unique in the context of most previous studies of sexual selection. First, they have evolved an intromittent organ independently of other well-studied taxa, such as insects, spiders, and mammals. Second, the lack of long-range perception mechanisms reduces the window of opportunity for males and females to exchange information during the very short period between the first contact and intromission. In some cases, however,

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acceptance or rejection of a mate may be based on information gathered before contact, such as the quality of the male territory or the presence of eggs in his nest. Regardless of the role of pre-copulatory interactions, actual fertilization success is likely to be strongly dependent on the outcome of copulatory and post-copulatory processes. In this sense, the fact that most species are highly promiscuous and have sperm cells that lack flagella, which are stored near to the tip of the ovipositor and used to fertilize eggs immediately before oviposition, renders Opiliones a fertile ground to study the role of cryptic female choice, sperm competition, and sexual conflict.

7.1 Introduction

The order Opiliones is a major group of arachnids that comprises nearly 6,500 species distributed in all continents, except for Antarctica (Machado et al. 2007; Kury 2012). The order is divided into four living suborders (Fig. 7.1a), whose species show marked differences in morphology and behavior. The suborder Cyphophthalmi is composed of nearly 190 small-bodied (1–3 mm in body length), short-legged species (Giribet 2007; Kury 2012; Fig. 7.1b), in which sperm transfer occurs via spermatophore (Karaman 2005). The remaining three living suborders form a clade called Phalangida, defined among other characters by the presence of intromittent male genitalia (Shultz and Pinto-da-Rocha 2007). The suborder Eupnoi comprises nearly 1,800 species and includes the forms widely known as daddy longlegs (Cokendolpher et al. 2007; Kury 2012; Fig. 7.1c). The suborder Dyspnoi comprises nearly 350 species exhibiting great diversity of body plans (Gruber 2007; Kury 2012; Fig. 7.1d). Finally, the suborder Laniatores is the most diverse lineage, including nearly 4,200 species, typically bearing spiny pedipalps and legs that are sexually dimorphic (Kury 2007, 2012; Buzatto and Machado 2014; Fig. 7.1e).

The book Harvestmen: The Biology of Opiliones, published in 2007, was a landmark in our understanding about the morphology, systematics, behavior, and ecology of the group, synthesizing in a single volume all available information on harvestmen that was scattered in thousands of papers published in several idioms. Although the publication of the book is relatively recent, some chapters are already outdated as a consequence of fast advances in our knowledge in recent years. The subject "reproduction" is perhaps the most emblematic of such a fast advance. From 2007 to now, the existence of male dimorphism and alternative reproductive tactics has been discovered in many species (Buzatto and Machado 2014), several new cases of both maternal and paternal care have been described (Requena et al. 2013; Buzatto et al. 2013), correlates of male mating success have been investigated (e.g., Buzatto and Machado 2008; Nazareth and Machado 2010; Fowler-Finn et al. 2014), and the use of phylogenetic information to infer the evolution of sexually selected traits has increased (e.g., Burns et al. 2013; Buzatto et al. 2014).

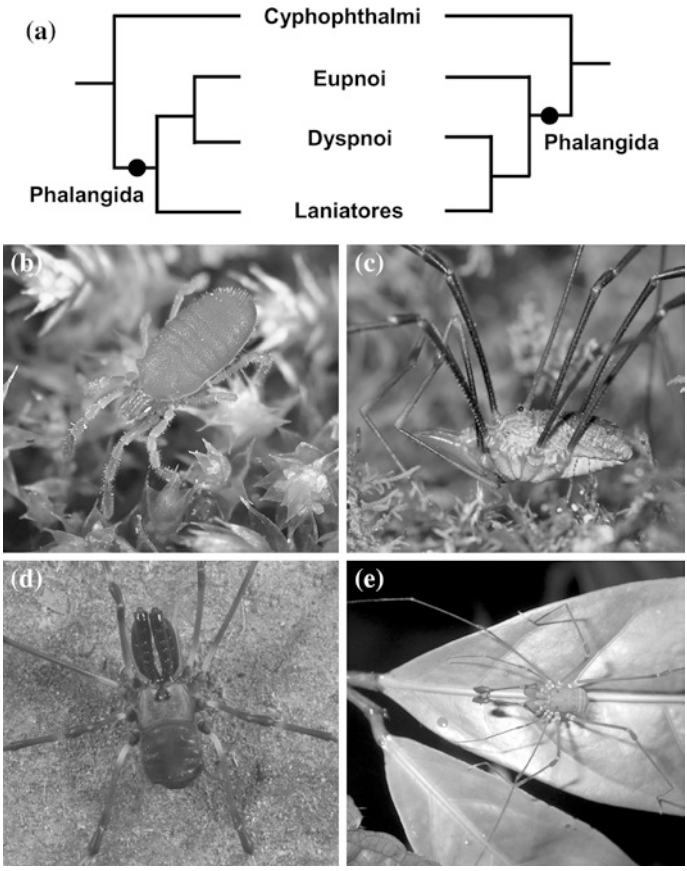

Fig. 7.1 **a** Two concurrent hypotheses for the relationship among the living suborders of Opiliones: *on the left side* Eupnoi + Dyspnoi form a clade called Palpatores, and *on the right side* Dyspnoi + Laniatores form a clade called Dyspnolaniatores (Giribet and Kury 2007). The two topologies recognize a clade called Phalangida that includes Eupnoi, Dyspnoi, and Laniatores. **b** Representative of Cyphophthalmi belonging to the family Sironidae (*photograph* Marshal Hedin). **c** Representative of Eupnoi belonging to the family Phalangiidae (*photograph* Daniel Proud). **d** Representative of Dyspnoi belonging to the family Ischyropsalididae (*photograph* Gonzalo Giribet). **e** Representative of Laniatores belonging to the family Stygnidae (*photograph* Glauco Machado)

Despite the great leap forward in the last seven years, there are still many gaps in our knowledge, and for the great majority of harvestman species, the only available information is the taxonomic description. Moreover, there is great geographic bias in our knowledge about harvestman behavior. Contrary to nearly all other animal groups, the reproductive behavior of harvestmen is better studied in the neotropics and southern temperate regions than in northern temperate regions (Buzatto et al. 2013). Considering that the diversity of the suborders is not evenly

distributed in the world (Kury 2012), the geographic bias also implies strong taxonomic bias. Finally, regardless of the region or taxonomic group, most of the studies on sexual selection in harvestmen conducted to date are devoted to describe patterns rather than to investigate mechanisms. Therefore, hard data or experimental evidence on cryptic female choice (CFC), sexual antagonistic coevolution, and sperm competition, for instance, are virtually absent.

If there is no such information on harvestmen, what should readers expect to find in this chapter? We will review the current information on sexual selection in harvestmen, focusing mostly on intersexual interactions (for an updated account on intrasexual selection, see Buzatto and Machado 2014). As we intend to show here, harvestmen are an interesting group to study sexual selection in general and CFC in particular, because they have evolved an intromittent organ independently of other taxa, such as spiders, insects, and mammals (Dunlop 2007; Macías-Ordóñez et al. 2010). Moreover, contrary to most species of these well-studied groups, in which long-range sexual information is exchanged in the form of exaggerated structures, colored ornaments, elaborate songs, or potent airborne pheromones, the great majority of harvestman species seems incapable of forming images, only perceiving changes in light intensity (Curtis 1970; Willemart et al. 2009). Although there is increasing evidence that harvestmen rub body parts against the substrate (Fernandes and Willemart 2014), probably leaving chemicals behind, they seem to be unable to detect long-range, vibratory or airborne chemical information (Edgar 1963; Willemart and Chelini 2007). However, their legs, especially the first two pairs, and sometimes their pedipalps, are equipped with sensitive contact chemo- and mechanoreceptors (Willemart et al. 2009). The complexity of their sensory mechanisms can be exemplified by a recent study that identified nine different sensory structures on the tegument of both male and females of *Dicranopalpus ramosus* (Eupnoi), with clear sexually dimorphic distribution throughout their legs, pedipalps, and chelicerae (Wijnhoven 2013). Sexual communication in animals that rely mainly on tactile or short-range chemical cues has been greatly overlooked, and here, we will explore the implications of the unique sensory system of harvestmen in a sexual selection context.

The chapter is divided into six major sections. In the first section, we provide an overview of harvestmen mating systems, which we consider the scenario for the sexual interactions we describe afterward. The following three sections explore the temporal sequence of male–female interactions, starting with a pre-copulatory phase, passing through the copulatory phase in which we focus on genital interactions, and finishing with the post-copulatory phase (Fig. 7.2). Then, we will explore cases of partial or total sex role reversal, focusing on male mate choice and female courtship behavior. Finally, we will conclude indicating the points that make harvestmen special for the study of sexual selection, with special emphasis on CFC, and will also suggest potentially promising research questions.

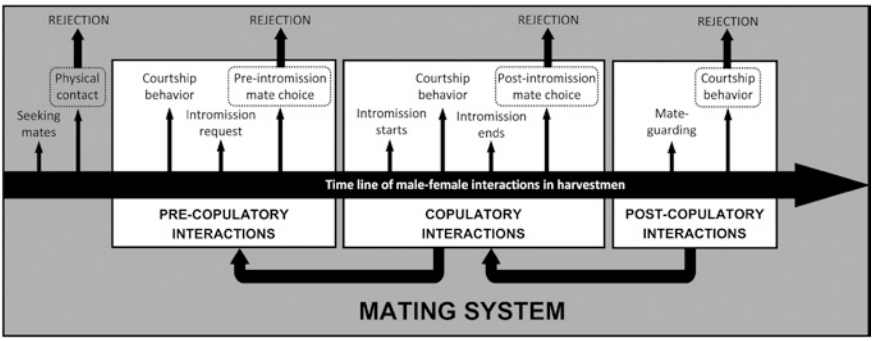

Fig. 7.2 Scheme of the chronological order of events during male–female interactions in harvestmen. Ecological and historical characteristics of populations determine the mating systems (*gray area*), which sets the specific rules of how and by which sex the reproductive behaviors are performed. Due to the harvestman sensory mechanisms, mating interactions only start after individuals find each other and establish physical contact. The whole mating process can be divided into three stages (depicted as *white boxes*): pre-copulatory, copulatory, and post-copulatory. Rejection of the mating partner may occur at different moments, which are highlighted by the *dotted line*. Multiple intromissions are common in species of the suborder Eupnoi, and this behavioral pattern is represented here by the *black arrow* connecting the pre- and copulatory stages at the bottom of the scheme. In some species of the suborder Laniatores, remating frequently occurs during mate guarding, and this behavioral pattern is represented here by the *black arrow* connecting the post- and copulatory stages at the bottom of the scheme

7.2 Mating Systems

7.2.1 General Characterization

Describing mating systems is important to address sexual selection in any group because they describe the set of reproductive strategies present in a given population (Emlen and Oring 1977) and thus the social context in which males and females can exert reproductive decisions (Fig. 7.2). There are several studies devoted to harvestmen reproductive biology (review in Machado and Macías-Ordóñez 2007), but only a few accounts provide details on their mating systems. Buzatto et al. (2013) provide a review on what it is currently known about harvestman mating systems, and here, we only summarize their main findings. Most harvestman species reproduce sexually, and, unlike other arachnids, they are highly polygynandrous, i.e., both males and females engage in copulation with multiple mates throughout the breeding season (Machado and Macías-Ordóñez 2007). The most likely mating system of species belonging to the suborders Cyphophthalmi and Dyspnoi, as well as many species of the suborder Eupnoi, is scramble competition polygyny (Buzatto et al. 2013), which involves multiple mating events for both males and females. In these groups, females generally lay eggs on sites that cannot be profitably monopolized by males, such as the bark of trees, leaf litter, cracks on rock walls, and empty snail shells (Machado and

Macías-Ordóñez 2007). Additionally, in several species with scramble competition polygyny, males offer nuptial gifts to their partners during courtship. These nuptial gifts are glandular secretions produced either on the base of the male's chelicerae and delivered directly to the female's mouth before intromission or on the base of the penis where females feed during intromission (see Pre-copulatory interactions below). Although there are some records of male–male fights for the possession of receptive females among species with scramble competition polygyny (e.g., Pabst 1953; Parisot 1962; Edgar 1971), males rarely exhibit enlarged armaments and there is no evidence of alternative mating tactics (Buzatto and Machado 2014).

Resource defense polygyny is a common mating system among species of the suborder Laniatores, but a few cases have also been reported among Eupnoi. In both suborders, males fight each other for the possession of reproductive territories that are visited by females looking for particular oviposition sites. These reproductive territories include natural cavities on trunks and riverside banks (Machado et al. 2004; Nazareth and Machado 2010), rocks (Macías-Ordóñez 1997, 2000; Zatz et al. 2011), specific host plants (Buzatto and Machado 2008), or mud nests built by males (Rodríguez and Guerrero 1976). In some species, females remain inside the male's territory after oviposition, forming harems that may include as much as ten females (Buzatto and Machado 2008; Zatz et al. 2011). In other species, females abandon the male's territory after oviposition, leaving their eggs hidden either inside small crevices (Macías-Ordóñez 1997, 2000; Wijnhoven 2011) or under the male's guard (Mora 1990; Nazareth and Machado 2010). Post-copulatory association between male and female is widespread in the order (see Post-copulatory interactions below), but it seems to be particularly common among species exhibiting resource defense polygyny (Buzatto et al. 2013) and/or exclusive paternal care (Requena et al. 2013).

Another feature that seems to be widespread among species exhibiting resource defense polygyny is the presence of alternative reproductive tactics, often associated with male dimorphism (Buzatto and Machado 2014). Large males (commonly referred to as majors or territorials) fight for the possession of reproductive territories or harems using elaborate weaponry. At least among gonyleptids, these weapons frequently include apophyses growing from the carapace or from one or more segments of their legs, especially the fourth pair. In some species, however, the whole leg is extremely elongated and functions as a whip in male–male contests. On the other hand, small males (commonly referred to as minors or sneakers) have reduced or completely absent weaponry and usually sneak copulations invading majors' territories (Buzatto and Machado 2014). The presence of two male morphs with different mating tactics in the population has profound implications for sexual selection (Kvarnemo and Simmons 2013), influencing the level of sperm competition (Muniz et al. 2014) and the level of sexual conflict within and between sexes (Buzatto and Machado 2014). However, these subjects have been poorly explored in harvestmen.

7.2.2 Potential for Female Mate Choice

Among polygynous populations, the freedom females have to perform mate choice is partially determined by the type of male–female associations. When females acquire resources on their own, they are free to choose among available males based on phenotypic differences (Borgia 1979). This situation occurs in male dominance polygyny (such as leks) and in some types of scramble competition polygyny. As far as we know, there is no case of lek among harvestmen, probably because the great majority of the species of the order is unable to form images and is very limited in the use of long-range chemical, vibratory, and acoustic stimuli (Willemart et al. 2009). On the other hand, no study conducted so far has investigated female choice in harvestman species exhibiting scramble competition polygyny, despite the fact that this is probably the most common mating system in the order (Buzatto et al. 2013). In the family Trogulidae (Dyspnoi), for instance, males search for receptive females and pre-copulatory and copulatory interactions involve mutual cheliceral rubbing and male leg tapping on the female's body (Pabst 1953). Given that trogulids, as well as many other harvestman species exhibiting scramble competition polygyny, are easily maintained in captivity (where females copulate and lay eggs), future studies should investigate whether specific morphological and behavioral traits in males influence their mating and fertilization success.

When males control reproductive resources, such as oviposition sites, females only have access to these resources by mating with the males controlling them (Borgia 1979). In this situation, typical of resource defense polygyny (associated or not with exclusive paternal care), females may actively choose mates based on resource quality and/or male phenotypic attributes, such as body size, weapon size, conspicuousness of ornaments, concentration of pheromones, or rates of displays. Alternatively, females may choose mates passively, which occurs when any female trait (morphological or behavioral) promotes or intensifies male–male competition, increasing females' chance of mating with a successful competitor (Wiley and Poston 1996). Passive female choice may be common among harvestman species exhibiting site or resource defense polygyny. Females of the harvestman *Zygopachylus albomarginis* (Laniatores), for instance, copulate exclusively with males associated with cup-like mud nests used as oviposition sites (Mora 1990). Therefore, by choosing where to lay their eggs, females of *Z. albomarginis* may passively select traits that indicate male ability to build, maintain, or even take over nests.

Females of the harvestman *Serracutisoma proximum* (Laniatores) lay eggs on the vegetation at river margins, showing marked preference for certain plant species. Preferred plants are predictable resources searched by females at the time of breeding, so that males benefit from defending and monopolizing territories containing these plants as a means of acquiring mates (Buzatto and Machado 2008). Since males use legs II as weapons to resolve contests for the possession of territories, the reported positive correlation between male leg length and number of

females in his harem may have emerged as a consequence of two non-mutually exclusive processes. First, since males owning territories are likely to be under intense intrasexual competition, females that mate with these males may benefit from producing offspring fathered by the best competitors. The hypothesis of passive mate choice would require a further correlation between harem quality and female choice, because the higher the quality of oviposition sites, the more intense male–male contests should be. However, variation in harem quality in *S. proximum* does not explain variation in the number of females found across harems (Buzatto and Machado 2008), and thus, this hypothesis has no empirical support so far. Second, females may actively choose males with longer legs II if this trait is genetically correlated with males' viability (good genes hypothesis) or increases the mating success of their sons due to the hereditary covariance between male trait and female preference (sexy sons hypothesis). Although it is hard to disentangle these two possibilities (Kotiaho and Puurtinen 2007), information on the correlation between male leg length and the fitness of his offspring, as well as on the genetic covariance between female preference and male leg length, may indicate the relative importance of these two different processes for the maintenance of the observed patterns.

When males directly monopolize females instead of territories, females may choose males actively, using phenotypic traits, or passively, if many receptive females aggregate in particular sites and males that better defend harems against competitors accumulate in the owner position (Borgia 1979; Wiley and Poston 1996). As far as we know, this mating system, known as female defense polygyny, has been reported for a single harvestman species, *S. proximum*. After the arrival of several females in a harem, territorial males concentrate their patrolling activity mostly on egg-guarding females. At this stage, the mating system seems to shift from resource defense to female defense polygyny (Buzatto and Machado 2008), and the most likely explanation for this shift relies in the gonadotrophic cycle of *S. proximum* females. Although females lay nearly 80–90 % of the eggs in the first 24 h after copulation, they may take up to 14 days to complete oviposition. This asynchronous egg deposition increases the possibility of polyandry, which could bring benefits for females, such as increased genetic variability in the offspring (Arnqvist and Nilsson 2000). However, by directly associating with egg-guarding females after the first oviposition bout, territorial males can increase their chance of fertilizing additional eggs retained in the females' ovaries and can also reduce the copulation success of males of a small morph (sneakers) that invade their territory (Buzatto et al. 2011; see also Post-copulatory interactions below). The extent to which mate-guarding behavior can influence female fitness and the potential conflict over promiscuity level between the sexes is an interesting area for future studies.

Finally, when males provide food resources to females in exchange for copulation or when males care for the offspring alone, females can choose males in terms of resource quality and/or direct or indirect benefits to the offspring (Borgia 1979; Hoelzer 1989). In harvestmen of the genera *Ischyropsalis* and *Paranemastoma* (Dyspnoi), for instance, males offer glandular secretions as a nuptial gift to

females before intromission, but the role of this secretion for female mate choice is still unknown (Martens 1969; Meijer 1972). Harvestman species exhibiting exclusive paternal care, in turn, have received increasing attention in recent years, and some information on female mate choice is now available (Requena et al. 2013). Given that paternal care minimizes the foraging costs related to egg guarding by females and may also provide information about the quality of paternal care, males providing care should be chosen by females and obtain a greater number of copulations than males that are not associated with eggs (Hoelzer 1989; Tallamy 2000, 2001). In fact, there is experimental evidence showing that females of *Magnispina neptunus* (Laniatores) consistently prefer to lay eggs inside nests that already contain eggs, regardless of individual male traits. Not surprisingly, males that usurp a nest containing eggs usually protect these eggs against predation (Nazareth and Machado 2010), and this egg adoption behavior probably increases the chance of acquiring their own eggs later.

Considering that the production of nuptial gifts (Vahed 1998; Gwynne 2008) and paternal care in arthropods (Requena et al. 2013) can be energetically expensive, passive female choice based on intense male–male competition is unlikely because any investment in weaponry may trade off the investment in food resource or parental behavior, reducing the direct benefits of female choice (Price et al. 1993). On the other hand, mate preferences based on the presence of eggs under a male's guard are the equivalent of passive female choice based on copying the decision of other females (sensu Dugatkin 1992) and may additionally benefit females by reducing the costs of mate search and assessment (Trumbo 1996). However, given that consistency and reliability of male care quality signals are crucial to determine female decisions (e.g., Hoelzer 1989; Price et al. 1993; Wagner 2011), the relative importance of active and passive female choice on males' reproductive success should respond to ecological and social factors affecting the costs paid by parental males (Requena et al. 2013). Considering that exclusive paternal care has evolved several times independently in harvestmen, the group offers a unique opportunity to test this hypothesis using a comparative approach.

7.3 Pre-copulatory Interactions

7.3.1 General Characterization

Courtship in most arachnids is a process that generally requires careful approach from males and long distance, elaborated, highly stereotyped, and species-specific visual or vibratory displays because females may attack and cannibalize approaching partners before copulation (Thomas and Zeh 1984). However, pre-copulatory cannibalism has never been recorded in harvestmen (Acosta and Machado 2007), and in most species, males seem unable to detect females until direct physical contact is established (e.g., Willemart et al. 2006; Fowler-Finn et al. 2014). Once male

and female detect each other, pre-copulatory interactions are generally brief and involve mostly tactile and close range chemical stimuli (Machado and Macías-Ordóñez 2007; Fig. 7.2). After the first contact, the mating pair generally adopts a face-to-face position, and males of many species of Eupnoi and Laniatores grasp the female using their pedipalps. In some species of Eupnoi, the male hooks his long, sexually dimorphic pedipalps at the base of female's second pair of legs (e.g., Edgar 1971; Macías-Ordóñez 1997; Burns et al. 2013; Fowler-Finn et al. 2014; Fig. 7.3a). In Laniatores, males grasp the females' pedipalps (Fig. 7.4a), but sexual dimorphism in the length or armature of the pedipalps is rare in species of this suborder (Macías-Ordóñez et al. 2010). Pedipalpal grasping has not been described for any species of Dyspnoi (Machado and Macías-Ordóñez 2007).

An active role of the male genitalia in male–female interactions in the pre-copulatory phase, prior to actual genital contact, is another unique feature of mating interactions in harvestmen. In some species of *Leiobunum* (Eupnoi), for instance, the pre-copulatory phase is characterized by the transference of secretions produced in glands located on the penis, in a region that is contacted by the female's mouth before and during intromission (Willemart et al. 2006; Macías-Ordóñez et al. 2010; Burns et al. 2013; Fowler-Finn et al. 2014). Therefore, we will use the term eversion to designate genital exposure of the penis prior to entering the female's genital opening and intromission as the actual insertion through such structure, but not necessarily through the female's vagina placed at the tip of the female ovipositor (for more details on genital interactions, see Copulatory interactions below).

7.3.2 Tactile Courtship and Nuptial Gifts

Sexual selection theory predicts that, unless males have some investment at stake in terms of material resources and/or time (see Male mate choice below), they should seek intromission soon after the first contact. Females, on the other hand, should carefully evaluate and reject some partners before intromission, unless they have full control of the fate of the sperm they receive (Andersson 1994). Most reports of pre-copulatory interactions in harvestmen indeed mention lack of evident courtship by males and some female reluctance before intromission (e.g., Roters 1944; Cloudsley-Thompson 1948; Parisot 1962; Edgar 1971; Macías-Ordóñez 1997; Fig. 7.2). Females of many species of Eupnoi and Laniatores seem to resist male advances by fleeing away or lowering their frontal end and placing the genital operculum close or in contact with the substrate, which makes intromission impossible (Machado and Macías-Ordóñez 2007; Fig. 7.3b). Nevertheless, in many species of these two suborders, the male taps different parts of the female's body using his front legs, while pedipalpal grasping is maintained (Willemart et al. 2006; Machado and Macías-Ordóñez 2007; Nazareth and Machado 2009; Fowler-Finn et al. 2014). Although it is short, the period between the first contact and intromission may be a phase of intense courtship because once a male and a female establish physical contact, the sensitive chemo- and

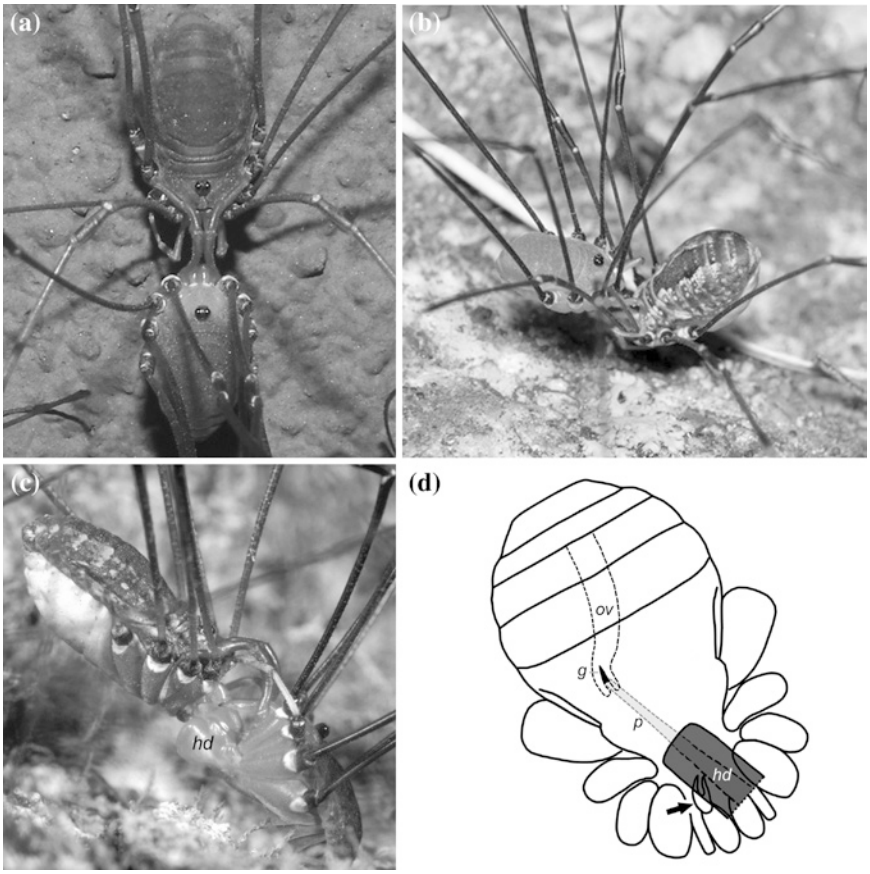

Fig. 7.3 **a** Mating pair of an unidentified Sclerosomatidae (Eupnoi) showing the male (*below*) grasping the female's first pair of legs using his pedipalps (photograph: Jerry Armstrong). **b** Female of *Leiobunum* (*right*) rejecting a male lowering the frontal end of her body so that intromission is impossible (photograph: Michael Marlow). **c** Lateral view of a mating pair of *Leiobunum* during intromission; the male is at the right, and *hd* indicates the inflated hematodocha, whose dorsal surface forms a conduit from basal nuptial glands to the female's mouth (*photograph* Joseph G. Warfel). **d** Schematic representation of the genital interaction in the same mating pair illustrated in **c**. The body of the female (*ventral view*) is outlined in *black* and her ovipositor (ov), which is retracted inside her body, is depicted by a *dashed black line*. Only the male's penis is outlined, with its tip (glans, g) depicted in *black* and the inflated hematodocha (hd), in *dark gray*. Note that (1) the penis only reaches the tip of the ovipositor below the vagina in the region where seminal receptacles are located, and (2) the female chelicerae are in close contact with the hematodocha (*black arrow*), probably feeding on glandular secretions

mechanoreceptors on their legs probably allow abundant flow of information by means of chemical and tactile stimuli. Moreover, mutual assessment of male and/or female relative body size may play an important role during pedipalpal grasping and pre-copulatory struggles (see below).

Fig. 7.4 **a** Mating pair of an unidentified Tithaeidae (Laniatores) in a forest in Singapore (photograph: Melvyn Yeo). Note that the male (*right*) uses his pedipalps to grasp the female's pedipalps during intromission. The *arrow* indicates the penis. **b** Male of *Serracutiosma proximum* (Laniatores) mate guarding an ovipositing female (photograph: Bruno A. Buzatto). The male (*above*) maintains his second pair of legs extended toward her and occasionally touches her legs or dorsum

A recent captivity study with *Leiobunum vittatum* (Eupnoi) investigated the influence of multiple male traits on the outcome of staged mating interactions (Fowler-Finn et al. 2014). Shortly after contacting the female, the male vigorously attempted to secure her in a mating embrace, typically wrapping the distal portion of his third pair of legs on the femur of her second pair of legs. During these initial pre-copulatory interactions, females were able to resist male mating attempts in more than half of the mating trials, even when males engaged in pedipalpal grasping (Fowler-Finn et al. 2014). Males that succeeded in starting the mating embrace had shorter pedipalps than unsuccessful males, and the authors suggest that the length of this appendage is decisive to the outcome of the male–female struggle: short pedipalps would provide greater mechanical advantage to overcome female resistance. While pedipalp length did not correlate with male body size, successful males that were larger compared to females were able to achieve intromission in just a few seconds, while smaller males spent much longer in this stage (Fowler-Finn et al. 2014). The relative importance of specific male traits (e.g., pedipalp length and body size) in overcoming female resistance and/or in signaling male quality, however, is still an open question that deserves future attention (Machado and Macías-Ordóñez 2007).

The total time males and females remain in contact before intromission corresponds to the window of opportunity for pre-copulatory courtship and thus female evaluation. In a well-studied clade of North American Eupnoi, the duration of pre-copulatory interactions shows great differences between sacculate and non-sacculate species (Burns et al. 2013). Sacculate species are those in which the penis has

a subterminal pair of cuticular sacs used for delivering a glandular secretion to the females before intromission. Females spend a few seconds or minutes feeding on this secretion, after which they may accept or reject intromission (Macías-Ordóñez et al. 2010). In non-sacculate species, little, if any, glandular secretion is transferred before intromission, and male pedipalps seem to be selected for strongly grasping the female. Moreover, in non-sacculate species, the pregenital opening of females is sclerotized and apparently serves as a barrier against forced intromission (Burns et al. 2013). The duration of the pre-copulatory phase in the non-sacculate species can last for up to 1 h, with periods of wrestling in which the male seems to forcefully penetrate the female's pregenital opening (Macías-Ordóñez et al. 2010; Burns et al. 2013). Therefore, males of non-sacculate species seem to rely more on a powerful grasping to negotiate with the female and less on pre-copulatory courtship, including nuptial gifts. We must highlight, however, that females of both sacculate and non-sacculate species do not commit to fertilization of their gametes by merely accepting copulation (see Copulatory interactions below).

Results of a phylogenetic comparative study show that loss of penile sacs and elaboration of male pedipalps are correlated in the clade of Eupnoi mentioned above, which includes species of the genera *Leiobunum*, *Eumesosoma*, and *Hadrobunus*. Moreover, the loss of penile sacs is also correlated with the gain of pregenital barriers in females (Burns et al. 2013), suggesting that male and female morphology coevolved in the group, probably in response to sexual selection during pre-copulatory interactions. A similar result has also been found in Japanese species of the curvipalpe group of *Leiobunum*. Males of species in which females may reproduce parthenogenetically (*L. manubriatum* and *L. globosum*) have larger and more powerful pedipalps than species with exclusive sexual reproduction, presumably as a result of selection to counteract female possibilities to reproduce asexually (Tsurusaki 2004). In the concluding remarks, we are going to explore the role of female choice, male–male competition, and intersexual antagonism for the emergence of the coevolutionary patterns described here.

As we stated before, pre-copulatory interactions in some species of Dyspnoi also include the transference of secretions, but in this case, they are produced in a pair of glands located dorsally on the first segment of the male chelicerae, which are either offered or somewhat forced into the female's mouth before intromission (Martens 1969; see also Fig. 12.3a in Machado and Macías-Ordóñez 2007). Although the composition, amount, and quality of the secretion offered by males in the suborders Eupnoi and Dyspnoi may influence the donors mating success and paternity, no study has investigated these questions in nuptial gift-giving harvestmen so far. An unpublished record under natural conditions shows two males of *L. vittatum* exhibiting pedipalpal grasping, one of them seemingly mimicking female stimulation on the other male's genitalia and obtaining the secreted nuptial gift, obviously without intromission involved (R. Macías-Ordóñez, unpub. data). This isolated observation, though anecdotal, suggests that glandular secretions in Eupnoi are valuable and/or nutritive. If these glandular secretions were only exploiting a sensory bias in females, other males should not be expected to cheat in order to feed on this secretion.

Recent observations with *Discocyrtus prospicuus* (Laniatores) show complex and still poorly understood pre-copulatory interactions (Stanley and Toscano-Gadea 2011). In this species, males approach females slowly waving the second pair of legs in front of their bodies. When individuals establish physical contact, the male slightly raises the front of his body and begins to evert and retract his penis. The female touches the penis with her first pair of legs for up to 1 min. No contact between the penis and the female's mouth has ever been recorded, and the first pair of female's legs is not inserted in her mouth after contacting the penis. Therefore, if there is some chemical signal during male–female interactions, it does not fit the definition of a nuptial gift, which implies the transference of food items or inedible tokens from males to females prior to or during copulation (sensu LeBas and Hockham 2005). After touching the penis of the potential mating partner, the female generally lowers her pedipalps allowing the male to perform cheliceral and pedipalpal grasping. All cases of male rejection ($n = 10$ observations) occurred when he attempted to grab the female without allowing her to touch the penis. In these cases of rejection, the behavior was similar to other harvestman species, with the female lowering the frontal end and approaching her venter to the substrate, preventing male access to her genital opening. It seems, therefore, that females use information acquired when touching the penis to evaluate their partners, but the type of information used remains to be investigated.

7.4 Copulatory Interactions

7.4.1 General Characterization

As far as we know, all harvestman species require direct male–female contact to transfer sperm. If there is an exception to this pattern, it should be found in the Cyphophthalmi, in which males of some species might leave spermatophores on the substrate for the female to find them, as occurs with some pseudoscorpions and collembolans (Proctor 1998). However, although only a few spermatophores have actually been recorded for species of Cyphophthalmi, the shape of the male genitalia and the way the spermatophores have been found attached to the female strongly suggest direct participation of the male during sperm transfer (Macías-Ordóñez et al. 2010). Moreover, results from a recent phylogeny of Opiliones including fossil species (Garwood et al. 2014) suggest that the presence of a spermatophore may be derived in Opiliones, which would contrast with all other major groups of arachnid, in which the spermatophore is plesiomorphic (Proctor 1998). Regardless of the evolutionary history of sperm transfer in the order, genitalic intromission is the rule in the suborders Eupnoi, Dyspnoi, and Laniatores, and direct interaction during intromission is well documented for a few species of these groups.

In species belonging to the clade Phalangida, both males and females may actively interact during intromission by touching, rubbing, tapping, grasping,

pushing, and pulling their partners in many ways with legs, pedipalps, chelicerae, and mouthparts (Willemart et al. 2006; Nazareth and Machado 2009; Macías-Ordóñez et al. 2010; Fowler-Finn et al. 2014; Fig. 7.2). As in the pre-copulatory phase, abundant chemical and tactile information probably flows during intromission, but we can do little but speculate about its meaning. Repeated intromissions while male pedipalpal grasping is maintained have been reported for many species of Eupnoi, but seem to be uncommon among representatives of Dyspnoi and Laniatores (Machado and Macías-Ordóñez 2007; Fig. 7.2). Along with scarce behavioral records, genital structure offers the basis to infer the potential processes that take place during male–female interactions during copulation. In the following topics, we summarize the available information on genital morphology and genital interactions in harvestmen. Our synthesis is largely based on Shultz and Pinto-da-Rocha (2007) and Macías-Ordóñez et al. (2010), to which the readers should refer for illustrations and further information.

7.4.2 Genital Morphology

The eversible genitalia of male Cyphophthalmi is called spermatopositor because it is much shorter than that of other harvestmen and appears to be used in the transfer of spermatophores rather than direct copulation (Van der Hammen 1985; Karaman 2005). The penis of the harvestmen belonging to the clade Phalangida is an intromittent organ typically divided into two main parts: pars basalis, which corresponds to most of the long shaft called truncus, and pars distalis, which contains the distal end of the truncus and the terminal or subterminal glans (Fig. 7.5). The pars distalis is the part that interacts with the ovipositor (Fig. 7.3c, d) and is often equipped with spines, sensilla, and other projections (Fig. 7.5). The glans is the most variable structure of the penis and contains the opening of the ejaculatory duct, located at the end of the stylus. Typically in Eupnoi and Dyspnoi, the pars distalis is composed almost exclusively of a relatively simple glans with an apical stylus, with the glans being only slightly differentiated from the truncus (Fig. 7.5a). In most species of Laniatores, however, the glans is very complex and can be divided into two main parts, capsula interna and capsula externa. The capsula interna is formed by sclerites associated with the distal end of the ejaculatory duct that are surrounded totally or partially by the capsula externa, formed simply by a soft sac called follis or by highly modified, sclerotized structures (Fig. 7.5b–h).

In muscular penises, the movement of the glans relative to the truncus is provided by one or two muscles that originate from the shaft and insert on a cuticular tendon that ends at the base of the glans. This muscular type of penis occurs in Eupnoi and Dyspnoi, as well as in two superfamilies of Laniatores, namely Travunioidea and Triaenonychoidea (Macías-Ordóñez et al. 2010). Representatives of the remaining superfamilies of Laniatores have hydraulic penises, i.e., the muscles are absent and the glans is apparently operated by

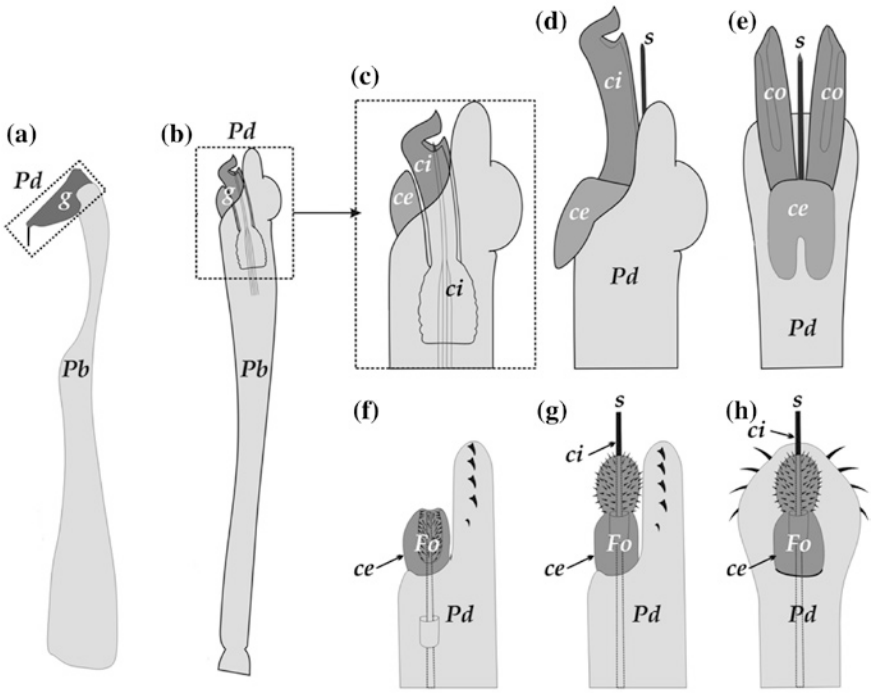

Fig. 7.5 Schematic representation of male genitalia in **a** Eupnoi and **b** Laniatores. The pars basalis (Pb) is a long shaft in both suborders, but the par distalis (Pd), especially the glans (g), is more complex in Laniatores. **c** Detail of the pars distalis in Biantidae (Laniatores) showing the capsula interna (ci) and capsula externa (ce). The capsula interna is everted by hydraulic pressure exposing the conductors (co), which are probably used to open the lumen of the ovipositor, and the stylus (s), in the tip of which is the opening of the ejaculatory duct: **d** lateral view and **e** frontal view. **f** Detail of the pars distalis in Assamiidae (Laniatores) showing the stylus retracted inside the capsula externa. When the follis (Fo) is everted by hydraulic pressure, the stylus is probably exposed inside the open lumen of the ovipositor: **g** lateral view and **h** frontal view. Modified from Macías-Ordóñez et al. (2010)

internal hemolymph pressure. It is important to note, however, that the terms muscular and hydraulic refer to the operation of the glans only. Eversion and inversion of the entire penis in all harvestmen are achieved by a combination of muscular and hydraulic mechanisms (Shultz and Pinto-da-Rocha 2007). Seminal products are apparently pushed through the long ejaculatory duct by a muscular propulsive organ located at the base of the penis; this organ is absent in Cyphophthalmi (Macías-Ordóñez et al. 2010).

The ovipositor in Cyphophthalmi and most Eupnoi has a shaft (sometimes as long as or longer than the female body) composed of cuticular rings connected by segmentally arranged muscles. It ends in paired bilateral processes derived from one or more rings, and the genital opening is located basally between these processes. Each process generally bears a tuft of sense organs on the latero-subdistal

surface. A pair of sclerotized seminal receptacles is found inside the genital opening, sometimes associated with glands (Martens 1986; see also Fig. 13.5 in Macías-Ordóñez et al. 2010). Lack of seminal receptacles is often associated with parthenogenesis (Shultz and Pinto-da-Rocha 2007). The ovipositors of Dyspnoi and Laniatores differ markedly from those of the other suborders. Their ovipositors are always much shorter than the female body and show marked structural differences such as circular muscles around the vagina, X-shaped lumen in cross section, and one or more short and sclerotized seminal receptacles in each of their four lobes (see Fig. 13.5 in Macías-Ordóñez et al. 2010).

7.4.3 Genital Interaction

Based on morphological and behavioral evidence, male and female genitalia interactions are likely to be greatly diverse in harvestmen. However, there are no detailed descriptions of genitalic interaction published for any species of Opiliones. Unpublished studies of *L. verrucosum* (Eupnoi) show that the stylus does not go beyond the first third of the ovipositor, where the openings of the seminal receptacles are located (J.W. Shultz, pers. comm.). Therefore, although a large portion of the penis shaft goes through the female's genital operculum, only its tip reaches the female reproductive tract since the ovipositor is retracted (Fig. 7.3c, d). This seems to be the general pattern for all harvestmen belonging to the clade Phalangida, and it is markedly different from other animal groups with internal fertilization, such as insects, birds, and mammals, in which the entrance to the female reproductive tract is continuous with the apparent external genital opening. Once inside the ovipositor, the glans in species of Eupnoi seems to have the appropriate shape and angle to enter the seminal receptacles after the ovipositor atrium, where it could release the sperm. With the stylus inserted in the seminal receptacles, the basal portion of the glans would lay near the tip of the ovipositor, seemingly in contact with the region containing abundant sensilla. This contact while the penis is reaching the seminal receptacle may suggest that the glans either stimulates females as a form of copulatory courtship or exploits female sensory bias by seductively stimulating the sensilla, used by females to probe optimal sites for oviposition (Macías-Ordóñez et al. 2010; see also concluding remarks below).

The penis in Dyspnoi and Eupnoi are fairly similar, but their ovipositors are strikingly different. The Dyspnoi ovipositor is shorter, and the seminal receptacles are smaller and highly variable in number. Detailed records of copulation for two species of *Ischyropsalis* (Dyspnoi) show a few short intromissions, while the female grasps and apparently feeds from the male's cheliceral glands (Martens 1969). The genitalic interaction during copulation, however, has never been described. Nevertheless, it seems that the Eupnoi-like penis with its stylus does not fit seminal receptacles in this suborder. The Dyspnoi penis seemingly leaves the sperm in the lumen of the ovipositor, still far from the sperm receptacles, where the female would need to somehow transport sperm to the seminal

receptacles or directly to the eggs. Moreover, the Dyspnoi ovipositor has fewer sensilla than the Eupnoi ovipositor and thus may be less sensitive to the stimulation of the penis.

Among the families of Laniatores, the modified morphology of the pars distalis shows very different arrangements of structures (Martens 1976, 1986), which apparently play three main roles during genital interactions (Macías-Ordóñez et al. 2010). First, they fasten the par distalis at the distal end of the ovipositor, where the seminal receptacles are located. Second, they seem to promote intromission of the penis in the ovipositor. Third, they may open the X-shaped vagina by hydraulic pressure and expose the stylus, which will release sperm in the lumen. The ringed muscles of the vagina in Laniatores may constrict the lumen so that the sperm transferred fill up the multiple seminal receptacles when it closes, after penis retraction. Such a muscular system might also enable females to reject sperm if the entrance to the seminal receptacles is obstructed. These hypotheses have never been tested, and an ongoing project with *Pachyloides throrelli* (Laniatores) may shed some light on sperm use and ejection in harvestmen (A. Pérez-González, pers. comm.). The ovipositors of Laniatores show fewer sensilla than other suborders, and the male genitalia possess a unique set of more proximal and highly variable and complex structures that seem in an ideal position to interact with the few sensilla. In contrast to the Eupnoi, in which males constantly move the body and the penis during multiple intromissions, in many species of Laniatores, the male's body remains motionless during the single intromission (Mora 1990; Buzatto and Machado 2008; Nazareth and Machado 2009, 2010; Requena and Machado 2014). Moreover, unlike Eupnoi males, which need to find the opening of the seminal receptacle to release sperm, Laniatores males may simply leave sperm in the lumen, passively entering into the multiple seminal receptacles through muscular contraction of the lumen (Macías-Ordóñez et al. 2010).

As explained above, the Laniatores penis does not go far inside the female reproductive tract, and sperm deposition is restricted to the tip of the ovipositor. It has been hypothesized that the function of a specific structure of the glans, known as ventral process (see Fig. 13.9 in Macías-Ordóñez et al. 2010), would be the removal of sperm from previous mates. The ventral process would penetrate the lumen of the ovipositor "brushing" the inner walls going in, but scraping off the same surface going out (Macías-Ordóñez et al. 2010). One important assumption of this hypothesis is that the sperm stored in the seminal receptacles should be transferred to the ovipositor lumen because the ventral process almost certainly does not enter these receptacles (A. Pérez González, pers. comm.). Moreover, because sperm removal is hypothesized to be a mechanical process, males would not discriminate between self and non-self ejaculates. Therefore, males should perform multiple intromissions, removing first the competitors' sperm and then transferring their own ejaculate later on. As far as we know, however, there is no obvious case of multiple intromissions in Laniatores. We argue, therefore, that a better understanding of sperm transfer and storage, as well as male–female genital interactions during intromission, is necessary to make stronger inferences on role of the ventral process and on the possibility of sperm removal in Laniatores.

Finally, lack of flagella in harvestmen sperm has important implications for post-copulatory processes in this group: their movement, if any, must be mostly controlled by female action. Once inside the seminal receptacles, being so close to the vagina at the tip of the ovipositor, their only movement may be restricted to exit seminal receptacles either by the flushing action of new sperm or by female control squeezing the seminal receptacles by contracting the ovipositor muscles. The later could potentially be done in the absence of any fertilizable egg as a means of spermatic rejection, or as mature eggs travel through the ovipositor and may come in contact with sperm just prior to crossing the vagina during oviposition, thus allowing fertilization (Macías-Ordóñez et al. 2010).

7.5 Post-copulatory Interactions

7.5.1 General Characterization

Male behavior after copulation shows great variation across Opiliones suborders. Anecdotal observations with a single species of Cyphophthalmi suggest that the male remains attached to the female after sperm transference, but additional information is necessary to understand this behavior (Schwendinger and Giribet 2005). Mating pairs in Dyspnoi generally do not show any post-copulatory interaction, and in some species, male and female may even flee from each other after copulation (Immel 1954). In Eupnoi and Laniatores, males of several species actively grasp or remain close to females until oviposition (Machado and Macías-Ordóñez 2007; Fig. 7.2). In *L. vittatum* (Eupnoi), for instance, the male wraps the female's legs using his own first pair of legs and follows her while she wanders inside his territory, apparently inspecting rock crevices for oviposition (see Fig. 12.2c in Machado and Macías-Ordóñez 2007). The male does not attempt to copulate again with the female during this association period and aggressively attacks any other approaching male. The post-copulatory association can last as much as 2 h and only ends when the female abandons the male's territory (Macías-Ordóñez 1997, 2000). In many species of Laniatores, females lay eggs immediately after copulation and males stay close to their mates during oviposition (Fig. 7.4b). Due to the great diversity of parental care forms in the suborder, a mating pair may remain together until the female abandons the clutch under the male's protection (Requena et al. 2013) or until the male returns to his activities as a territorial owner, leaving the eggs under female's protection (e.g., Machado and Oliveira 1998; Buzatto and Machado 2008). In both situations, post-copulatory associations may last more than 24 h, during which the male often attempts (and occasionally succeeds) to remate with the same female (Machado and Macías-Ordóñez 2007; Macías-Ordóñez et al. 2010).

The post-copulatory associations described here are not exclusive to harvestmen, and in many arthropod species, the mating pair remains together for periods longer than the necessary to transfer sufficient sperm to fertilize the eggs.

Alcock (1994) categorized the post-copulatory interactions of insects based on the extent of contact between male and female. According to this categorization, paired individuals may (1) keep genital contact for longer than needed for insemination; (2) exchange mating plugs, with males transferring secretions or even parts of his body that remain attached to female's genital opening; (3) keep body contact, usually with males grasping females using jaws, claspers, or legs; or (4) keep close proximity, with males apparently monitoring females without physical contact after copulation. Regarding category (1), intromission in harvestmen can last from few seconds in some Eupnoi to more than 10 min in some Dyspnoi and Laniatores (Macías-Ordóñez et al. 2010), but based on the scarce available data, it is not possible to say whether male and female keep genital contact for longer than needed for insemination. Category (2) does not apply to harvestmen, since there is no description of mating plug in the order. Nevertheless, mating pairs in Eupnoi and Laniatores may remain together after copulation, with males either grasping females with their front legs or guarding females at close proximity (Machado and Macías-Ordóñez 2007; Fig. 7.4b). In some species, males can also block the entrance of their nests, preventing females from leaving and other males from entering (Nazareth and Machado 2010). Therefore, we will explore categories (3) and (4), which are intersexual associations that may prevent females from remating and avoid sperm competition (i.e., mate guarding). These post-copulatory interactions may also prolong courtship signals that provide additional information to females (i.e., CFC) and protect female and/or offspring against natural enemies (i.e., direct benefits). All these possibilities are non-mutually exclusive, and we argue that researchers should consider multiple alternative predictions when designing experiments to understand the meaning of post-copulatory associations for both males and females (see below).

7.5.2 Mate Guarding

Prolonging association after sperm transference may benefit males by reducing the chances of the female accepting copulation with rival males, which would increase sperm competition due to the presence of additional ejaculates in the female's reproductive tract and potentially the removal of his sperm by female's subsequent mates (Alcock 1994; Simmons 2001). The key prediction of this hypothesis is that males exhibiting mate guarding should fertilize relatively more eggs than males that abandon their mates after copulation. To date, no experiment has been conducted with harvestmen to estimate males' fertilization success. Furthermore, molecular markers developed for a couple of species of Laniatores (AFLP: B.A. Buzatto, pers. comm.; microsatellites: G.S. Requena, unpub. data.) have shown surprisingly low levels of polymorphism within populations, preventing any reliable estimation of paternity. Therefore, advances in the techniques used to properly assign parentage are still needed for species of the order Opiliones.

A more complete analysis of the evolution and maintenance of mate guarding should consider the balance between male fitness benefits and costs associated with this behavior (Alcock 1994). Last male sperm precedence has been argued to be the main determinant of the benefits of mate guarding (Alcock 1994; Simmons 2001; Harts and Kokko 2013). The proportion of offspring sired by the last male to mate (usually referred to as P2) is a measure commonly used to infer fertilization mechanisms. Unfortunately, the same observed P2 pattern may be achieved by several alternative mechanisms biasing fertilization (see Simmons and Siva-Jothy 1998; Simmons 2001). For instance, Simmons (2001) lists six different processes that may increase P2, claiming that the underlying mechanisms are poorly understood and refined information about sperm dynamics during and after copulation is lacking for most species. Although direct quantification of P2 seems technically problematic in harvestmen, questions regarding mechanisms associated with the fertilization pattern of last male sperm precedence may be answered by characteristics of sperm biology. If post-copulatory association in harvestmen has evolved or has been maintained by sperm competition, the presence and the intensity of mate-guarding behavior should be related, for instance, to patterns of sperm longevity (e.g., Lessels and Birkhead 1990; Greeff and Parker 2000), sperm displacement (e.g., Parker and Simmons 1991; Parker et al. 2010), and sperm use and storage between reproductive events (Requena and Alonzo 2014).

Remaining with a female after sperm transference may also impose costs to males in terms of injury when repelling rival males or limited time available to invest in additional mates and territorial defense (Alcock 1994; Simmons 2001). Males of *L. vittatum* guarding females after copulation ignore other females and fight more vigorously than non-guarding males and commonly defeat approaching males (usually in less than 10 s), regardless of differences in body size or number of legs between contestants. Although the male never abandons his mate for additional mating opportunities with unattended females within his territory, the frequency of such additional encounters is low compared to additional mating opportunities after the mate-guarding period under natural conditions (Macías-Ordóñez 1997). Therefore, male mate guarding in *L. vittatum* may have been favored by a combination of low risks of injury (since agonistic interactions with conspecific males are quickly resolved), potentially low energetic costs of guarding (since males just follow females within their territories), and low reproductive costs due to small loss of mating opportunities.

In *S. proximum* (Laniatores), although territorial fights are common for the establishment of harems at the beginning of the breeding season, aggressive contests between males during the mate-guarding period have never been reported, and sneaker males quickly retreat if detected by territorial males (Buzatto et al. 2011). Therefore, the risk of injury of males during mate guarding in this species is probably very low as well. However, given that a territorial male can guard only one female at a time (Fig. 7.4b), as the number of females in his harem increases, it becomes more difficult to successfully defend all of them from sneakers. When the territorial male is copulating or mate guarding one female of his harem, sneakers can seize the opportunity to copulate with other unguarded females (Buzatto

et al. 2011). Considering that social factors, such as adult sex ratio, density, and relative frequency of sneakers, show great variation across populations of *S. proximum* (Munguía-Steyer et al. 2012), the costs-to-benefits ratio of mate guarding should also vary in different populations. In this sense, the mate-guarding hypothesis provides additional predictions on the relationship between the intensity of mate guarding and ecological pressures on males regarding the costs and benefits of this behavior (Alcock 1994). As far as we know, those predictions have never been tested, but harvestmen are an ideal group of organisms to study interpopulation variations in male post-copulatory behavior.

One last possibility, particular to some species in which males establish their nests and take care of the offspring inside natural cavities, is that males may block nest entrance after copulation so that females are prevented from leaving. This behavior has been frequently observed in captivity conditions for *M. neptunus* (Laniatores) (Nazareth and Machado 2010), but it may also exist in *Gonyleptes saprophilus* and *Neosodocus* sp. (Laniatores) (Machado et al. 2004; Requena et al. 2013). While the behavior of blocking nest entrance can result in paternity protection, by preventing females to mate with additional males before oviposition, males can also prevent females from leaving their nest, prolonging their permanence inside and perhaps increasing the number of eggs they lay. This situation creates the possibility of sexual conflict, depending on how male behavior may affect female fitness. If attempts of nest takeovers by competitor males or nest abandonment by the ovipositing female are likely, successfully sustaining the blocking behavior could provide additional information to females about male quality. On the other hand, if remaining inside the nest for long periods limits female foraging activity and/or decreases the benefits derived from polyandry (Kvarnemo and Simmons 2013), blocking behavior could impose fitness costs to females. How sensitive those costs and benefits are to variation in ecological conditions is an open question that still deserves attention.

7.5.3 Cryptic Female Choice

An additional explanation for remaining with the female after copulation is to prolong behavioral interactions between the mating pair, so that females would be able to assess complementary male traits during post-copulatory courtship stimulation and "decide" about sperm use (Eberhard 1996; Fig. 7.2). The key prediction of this hypothesis is that male reproductive success should be directly related to his behavioral performance during the post-copulatory period. In several species of Eupnoi and Laniatores, males grasp or tap females' body and legs after intromission (Machado and Macías-Ordóñez 2007). For instance, *L. vittatum* males tap the female's dorsum while holding her within his territory (Macías-Ordóñez 1997). Evidence for several species of Goniosomatinae (Laniatores) exhibiting maternal care shows that territorial males remain with females until they complete

oviposition, waving their second pair of legs and occasionally touching females' legs and dorsum (Gnaspini 1995; Machado and Oliveira 1998; Willemart and Gnaspini 2004; Buzatto and Machado 2008).

Despite the observational evidence of post-copulatory interactions between male and female in harvestmen, there is no study linking the post-copulatory performance of the males to the number of eggs sired by them. As discussed before, this gap in our knowledge may be explained in part by the challenge of estimating paternity in species of the order. Male post-copulatory performance, however, may also affect other components of his success that may provide circumstantial evidence of CFC. For instance, females may respond to intense male courtship behavior by reducing the interval between copulation and oviposition, increasing the number of eggs laid after the copulation, allocating additional resources into the eggs sired by the courting male, or simply staying for longer near that mating partner. Females of many harvestman species copulate and lay eggs in the laboratory, and it is relatively easy to manipulate the intensity of male courtship behavior by immobilizing their second pairs of legs and preventing them from touching their partners both during and after intromission. Therefore, these species are good models to investigate female behavioral response to varying intensities of male courtship both during and after intromission.

In species exhibiting exclusive paternal care, the post-copulatory association between the mated couple lasts until the end of oviposition and it is strictly necessary for males to provide care. Exclusive paternal care has independently evolved in at least nine lineages of Opiliones, all of them belonging to the suborder Laniatores. In all those lineages, females mature eggs continuously throughout the breeding season, and male care has been demonstrated to improve the survival of their clutches, which usually contain eggs laid by multiple females (Requena et al. 2013). The post-copulatory behavior of parental males varies across species, from sporadic touches on females' legs with the second pair of legs (Requena and Machado 2014) to active tapping on females' dorsum and venter with the first and second pair of legs (Mora 1990; Nazareth and Machado 2009, 2010). Moreover, females are also predicted to evaluate the prospective survival chances of the offspring to decide where to lay their own eggs (Sargent 1988; Hoelzer 1989; Tallamy 2001). For instance, the hygienic condition of a clutch of *Z. albomarginis* (Laniatores) may indicate the microclimatic quality of the oviposition site or the male ability to clean the eggs (Mora 1990). Additionally, ovipositing in clutches containing a large number of eggs may also benefit a female because her offspring would be protected by both the dilution effect during a predation attack (Sargent 1988) and the high quality of male protection (Hoelzer 1989; Tallamy 2001). Finally, when paternal activities are condition dependent, females should benefit by evaluating accurately and directly the current condition of guarding males (Requena et al. 2013). Therefore, depending on the context, characteristics of the broods themselves and/or directly of the males are expected to affect post-copulatory female decisions, which may be expressed not only in terms of biases in paternity, but also in the number of eggs laid or resource allocation.

7.5.4 Direct Benefits

The last explanation we explore for post-copulatory association in harvestmen considers the delivery of direct benefits from males to females. Under this perspective, by protecting females from predators or from the sexual harassment of rival conspecifics, a male would benefit from increasing the chances of his mate surviving to lay eggs sired by him (Alcock 1994). After copulation, females of *L. vittatum* may spend as much as 2 h in the male's territory inserting her ovipositor under the moss layer and inside rock crevices, probably selecting specific oviposition sites based on microclimatic conditions (Macías-Ordóñez 1997). Because territory owners maintain close contact with females while they are wandering in the territory and aggressively attack approaching males, female protection from sexual harassment during rock inspection and oviposition may confer direct benefits to the females (Machado and Macías-Ordóñez 2007). From the males' perspective, mate guarding may additionally protect their paternity by avoiding sperm competition, as discussed above.

Post-copulatory association between the mated couple may also improve males' reproductive success by directly increasing offspring survival due to helping females to provide parental care (Alcock 1994). Although there is no record of strict biparental care in any harvestmen, species with polygynous mating systems associated with maternal care can provide an equivalent scenario for male post-copulatory decisions. Territorial males of *S. proximum* patrol females that remain inside their harems after oviposition, in a period during which maternal care takes place (Buzatto and Machado 2008). When females abandon their eggs, either naturally or experimentally, some territorial males have been observed to care temporarily for unattended clutches within their harems (Buzatto and Machado 2009). Temporary male care in this species may be important for offspring survival (and hence female fitness) since egg predators usually consume entire clutches in just a few hours or days (Buzatto et al. 2007). This association, however, can be costly as it limits male patrolling behavior toward additional females in his harem and may compromise his ability to prevent sneaker males' invasion and copulation. As mentioned before, non-mutually exclusive mechanisms for post-copulatory association may be operating simultaneously and the balance between the costs and benefits to males of such association should be taken into account for a more complete appreciation of the processes driving male behavior evolution and maintenance.

7.6 Male Mate Choice

For a long time, the so-called Darwin–Bateman paradigm was the cornerstone of sexual selection theory, leading to three general predictions (Dewsbury 2005): (1) male reproductive success should vary more than that of females; (2) male reproductive success should be more influenced by the number of mating events than that of females; and (3) males should mate indiscriminately, while females should

be discriminating. However, in the last two decades, it has become clear that sex roles are dynamic and variable, with an increasing number of empirical works reporting male choosiness and female–female competition (Bonduriansky 2001; Edward and Chapman 2011). Moreover, recent studies have built up the theoretical framework to investigate the evolution of male mate choice (e.g., Servedio and Lande 2006; Barry and Kokko 2010; Edward and Chapman 2011). In this sense, one essential condition favoring male choosiness is the cost associated with male reproductive decisions. For instance, relatively inexpensive mate search and assessment would allow males to sample and evaluate a great number of receptive females before effectively mating. On the other hand, great investment in parental activities or nuptial gifts by males is likely to energetically constrain their allocation to mate with many females and/or to produce sufficient ejaculate, which is predicted to favor male discriminatory behavior. Other condition favoring the evolution of male mate choice is related to the benefits of choosiness. Great variation in viability or fecundity among females is predicted to increase the fitness advantages of male selectiveness in terms of the potential quality and quantity of offspring to be sired. The balance between the costs and the benefits of male mate choice should determine the net advantage of performing such behavior.

Although there are several nuptial gift-giving species in harvestmen (see Precopulatory interactions above), there is no reported case of sex role reversal, as those described for some orthopterans (Vahed 1998; Gwynne 2008). However, at least, some harvestman species exhibiting exclusive paternal care show evidence of male mate choice and we will explore these cases in more detail in the following topics. A comprehensive review of sex role reversal in harvestmen and other arthropods exhibiting exclusive paternal care is presented in Requena et al. (2013).

7.6.1 Males Repelling Females

Females of *Iporangaia pustulosa* (Laniatores) lay eggs on the vegetation, and males take care of the offspring during the entire period of embryonic development (Machado et al. 2004). Paternal care, however, does not seem to constrain mate acquisition: caring males can mate with as much as 15 females and take care of all of their eggs simultaneously in multiple clutches (Requena et al. 2012). Mate search is exclusively accomplished by females, who may visit several males over the course of the breeding season. Field observations show that caring males aggressively repel some females upon arrival, even before copulation (Requena and Machado 2014). One possible explanation for this behavior is that the high mating frequency of some males and the low food intake during the caring period (Requena et al. 2012) may jointly compromise sperm production and replenishment (Requena and Machado 2014), negatively affecting future mating opportunities (e.g., Härdling et al. 2008). Under this circumstance, males would benefit from evaluating the quality of the arriving females, which can be accomplished using close range volatile chemicals or contact hydrocarbons during the brief

pre-copulatory interactions (Requena and Machado 2014). Evaluating variation in traits signaling female fertility and sperm competition risk between rejected and accepted females, as well as sperm load in the seminal vesicle of males that accept and reject visiting females, is crucial to understand male selectivity in *I. pustulosa*.

Females of *Z. albomarginis* and *M. neptunus* (Laniatores) exclusively lay eggs inside nests that consist of cuplike structures built by males in the first case (Mora 1990) and natural cavities on roadside banks in the latter case (Nazareth and Machado 2010). Males of both species protect their nests against the invasion of conspecific males as well as egg predators, and behavioral observations show that they also attack some visiting females, biting their legs and chasing them out of the nest (Mora 1990; Nazareth and Machado 2010). Contrary to the pattern described for *I. pustulosa*, attacks in both species usually take place after males and females interact or even copulate. Additionally, territorial males of *Z. albomarginis* and *M. neptunus* use their second pair of legs to touch the venter of visiting females during such interactions (Nazareth and Machado 2010; G.S. Requena, unpub. data). Given that oviposition in Laniatores usually happens immediately after copulation (see Post-copulatory interactions above), males may touch females' venter to assess whether they everted the ovipositor and started oviposition. Considering that cannibalistic activities from conspecific females constitute an important source of egg mortality in harvestmen with paternal care (Mora 1990; Requena et al. 2009; Nazareth and Machado 2010), any delay in everting the ovipositor may indicate females' predatory intentions. In fact, cannibalistic females of *M. neptunus* first copulate with the guarding males and then attempt to eat some of the eggs while they are being courted by the guarding male (Nazareth and Machado 2010). Therefore, male attack toward females may represent a parental protective behavior, and manipulations of female feeding condition should help elucidating whether male aggression is preferentially directed to cannibalistic females.

7.6.2 Female Courtship and Aggressive Behaviors

Although *L. vittatum* (Eupnoi) shows conventional sex roles, females seem to court males during grasping by rubbing, pinching, and grasping the male genital opening and the genitalia using their chelicerae and pedipalps, prior to and during penis eversion and nuptial feeding. Furthermore, some sexual interactions may involve grasping, but not intromission, even when females do not seem reluctant to mate (R. Macías-Ordóñez, unpub. data). Males in this, and probably other nuptial gift-giving harvestman species, may have a choice of whether to offer glandular secretions and proceed with the copulatory sequence or not. Males may also modulate how much secretion they offer, if they are able to assess female quality. If so, some form of female courtship may be expected, but it may be really subtle and very detailed observations of the sexual interaction must be carried out to discover it. This scenario would also explain the possibility of cheater males mimicking female stimulation in order to obtain nuptial gifts as described above (see Pre-copulatory interactions).

In *Z. albomarginis*, nesting males remain most of the time inside their territories and females actively visit nests over the course of the breeding season. After approaching a nest, a female enters and taps the walls and the floor of the nest with the first pair of legs, and either abandons the nest or initiates courtship. In this second scenario, she taps the partner using her second pair of legs, moves around, and faces the male until he starts tapping her with his first legs, or biting and chasing her off the nest (Mora 1990). It seems that mate interactions in this species allow not only females to evaluate nests and males' qualities (see Post-copulatory interactions above), but also males to assess potential mates (Mora 1990). Although females usually abandon the clutch after oviposition (Rodríguez and Guerrero 1976), they sometimes spend several days in the vicinity of one or two nests, where they may engage into aggressive behaviors toward newcomer females that approach one of these nests (Mora 1990). Given that conspecific females are the main egg predators in *Z. albomarginis* (Mora 1990), the risk of cannibalism may also explain female–female aggression. Therefore, the partial sex role reversal of *Z. albomarginis* offers a remarkable opportunity to investigate not only the criteria used during mutual mate choice, but also the conditions favoring female strategies of male monopolization, a mating strategy extremely rare in nature.

7.7 Concluding Remarks

Several traits in harvestmen make them unique in the context of most previous studies of sexual selection. The lack of long-range perception mechanisms reduces the window of opportunity for males and females to exchange information during the very short period of close proximity or physical contact prior to intromission (Fig. 7.2). In some cases, however, acceptance or rejection of a mate may be based on information gathered even before contact. Although empirical data are scarce, we argue that this would be the case in harvestman species where: (a) individuals of one sex leave chemical cues on the substrate that may be used by individuals of the other sex to evaluate mate quality; (b) males defend specific oviposition sites, and females' mating decisions are based either on the direct assessment of territory quality or on the passive mate choice; or (c) males suffer from sperm depletion, and the acceptance or rejection of a female is primarily based on the amount of ejaculate males have in their seminal vesicles. Regardless of the role of pre-copulatory interactions, actual fertilization success is likely to be strongly dependent on the outcome of copulatory and post-copulatory processes. In this sense, the fact that most species are highly promiscuous and have sperm cells that lack flagella, which are stored near to the tip of the ovipositor and used to fertilize eggs immediately before oviposition (Macías-Ordóñez et al. 2010), renders Opiliones a fertile ground to study the role of CFC, sperm competition, and sexual conflict.

In the context of CFC, it is important to define when hypotheses are made on the original (ancestral) function of a trait involved in male–female interactions or on its current function, which may not only differ, but to some degree are expected

to change over time along the evolutionary history of a lineage (Eberhard 2004). The use of phylogenies to infer evolutionary changes in the function of traits under sexual selection is a powerful tool that has only recently been applied in Opiliones. For instance, the study by Burns et al. (2013) with a clade of Nearctic Eupnoi clearly shows that, in species in which males deliver a nuptial gift to the females before intromission, sexual dimorphism in the pedipalps is absent and females lack physical barriers in their genital operculum that seem to interfere with intromission in other species. On the other hand, in species in which males lack gift-giving glands, sexual dimorphism in the length of the pedipalps is well marked and females have structures that seem to function as barriers against intromission. The latter scenario constitutes the derived state and has evolved independently at least four times in the clade. Based on these results, the authors argue that female choice is the ancestral state and sexual conflict is a repeatedly evolved derived state. Furthermore, they hypothesize that major ecological factors, such as the length of the reproductive season, may trigger the change of state through three non-mutually exclusive mechanisms: (1) natural selection for male economy in nuptial gift production in extreme latitudes with shorter reproductive seasons, (2) a change of target trait of female choice from production of nuptial gifts to mechanical or stimulatory attributes of potential mates, and (3) stronger intrasexual selection among males under shorter mating seasons would result in selection for behavioral (e.g., mate guarding) or morphological (e.g., size or weapons) traits that could also be used on female coercion.

In conclusion, a male sexual trait may originate in a sexual conflict context, promoting evolutionary response of a wide array of female sexual traits and falling later in a female-screening evolutionary process (e.g., Macías-García and Ramirez 2005). Conversely, as suggested by Burns et al. (2013), a male sexual trait may have originally had a female courting function and then switched to a coercive one. Testing for these possibilities is a highly attractive research line, which requires a robust phylogenetic hypothesis on the study group, detailed studies on form and function, as well as detailed data on behavior in wild populations. Besides the uniqueness of Opiliones in the terms stated above, all these conditions have been developing in recent years, transforming the order in one of the most exciting and promising ones in terms of research opportunities in reproductive evolutionary ecology.

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