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Review

Reproductive biology of harvestmen (Arachnida: Opiliones): a review of a rapidly evolving research field

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Abstract

Harvestmen are a major arachnid order that has experienced a dramatic increase in biological knowledge in the 21st century. The publication of the book *Harvestmen: The Biology of Opiliones* in 2007 stimulated the development of many behavioral studies. Although the book is relatively recent, our understanding of the reproductive biology of harvestmen is already outdated due to the fast accumulation of new data. Our goal is to provide an updated review of the subject to serve as a benchmark for the following years. In the pre-copulatory phase, we explore the evolution of facultative parthenogenesis, the factors that may affect the types of mating system, and the role of nuptial gifts in courtship. Regarding the copulatory phase, harvestmen are unique arachnids because they have aflagellate spermatozoa and a penis with complex morphology. We discuss the implications of these two features for sperm competition and cryptic female choice. In the post-copulatory phase, we connect oviposition site selection and climate conditions to the widespread occurrence of resource defense polygyny, alternative reproductive tactics, and sexual dimorphism in several clades of tropical harvestmen. Finally, we present the different forms of parental care in the order, and discuss the benefits and costs of this behavior, which can be performed either by females or males. Throughout the review, we indicate gaps in our knowledge and subjects that deserve further studies. Hopefully, the information synthesized here will stimulate researchers worldwide to embrace harvestmen as a study system and to improve our effort to unravel the mysteries of their reproductive biology.

Key words: alternative reproductive tactics, nuptial gifts, parental care, parthenogenesis, resource defense polygyny, sexual dimorphism.

The publication of the book *Harvestmen: The Biology of Opiliones* in 2007 was a landmark in our comprehension of the systematics, biogeography, ecology, and behavior of harvestmen (Pinto-da-Rocha et al. 2007), an arachnid order with nearly 6,700 described species distributed across all continents, except Antarctica (Kury et al. 2021). The book summarized all available information, which was scattered in hundreds of publications from a dozen languages, some published in the late 19th and early 20th centuries. Although the book is relatively recent, some chapters are already outdated due to the increase in knowledge that has occurred in the last 15 years. The chapter on reproduction (Machado and Macías-Ordóñez 2007) is perhaps the most emblematic example of this outdating. Since the publication of the book, there has been an increase in the number of published papers of reproductive biology of harvestmen (Figure 1A), particularly those related to behavior and morphology (Figure 1B). More specifically, our knowledge on the causes and consequences of parthenogenesis has increased (e.g., Burns and Tsurusaki 2016; Burns et al. 2018; Brown et al. 2021), we discovered alternative reproductive tactics in several species (Buzatto and Machado 2014), and the first studies on genital interaction (Pérez-González and Werneck 2018), intra- and inter-specific variation in ovipositor morphology (Townsend et al. 2015), spermathecal morphology (Karachiwalla et al. 2020), nuptial gift chemistry (Kahn et al. 2018), and sperm competition (Munguía-Steyer et al. 2012; Townsend et al. 2019) have been published. Moreover, investigation of the factors that affect the reproductive success of males has begun (Buzatto and Machado 2008; Nazareth and Machado 2010; Fowler-Finn et al. 2014, 2018; Requena and Machado 2015), many new cases of maternal and paternal care have been described (Buzatto et al. 2013 and Requena et al. 2013), and the use of phylogenetic and phylogeographic information to answer questions related to the evolution of reproductive traits has increased (e.g., Burns et al. 2013, 2018; Buzatto et al. 2014; Machado et al. 2016).

The main goal of this article is to provide an updated review of the reproductive biology of harvestmen. The review is divided into three main sections: 1) the *precopulatory phase*, which includes the 2 types of reproduction (sexual and asexual), forms of mate acquisition, and the chemical and tactile interactions prior to intromission; 2) the *copulatory phase*, which involves the chemical and tactile interactions during copulation, genital stimulation, and sperm competition; and 3) the *postcopulatory phase*, which includes mate-guarding, oviposition site selection, and parental care. Due to the general nature of the review, we have selected examples from a wide variety of taxa within the order Opiliones and from localities worldwide. These examples illustrate the diversity of

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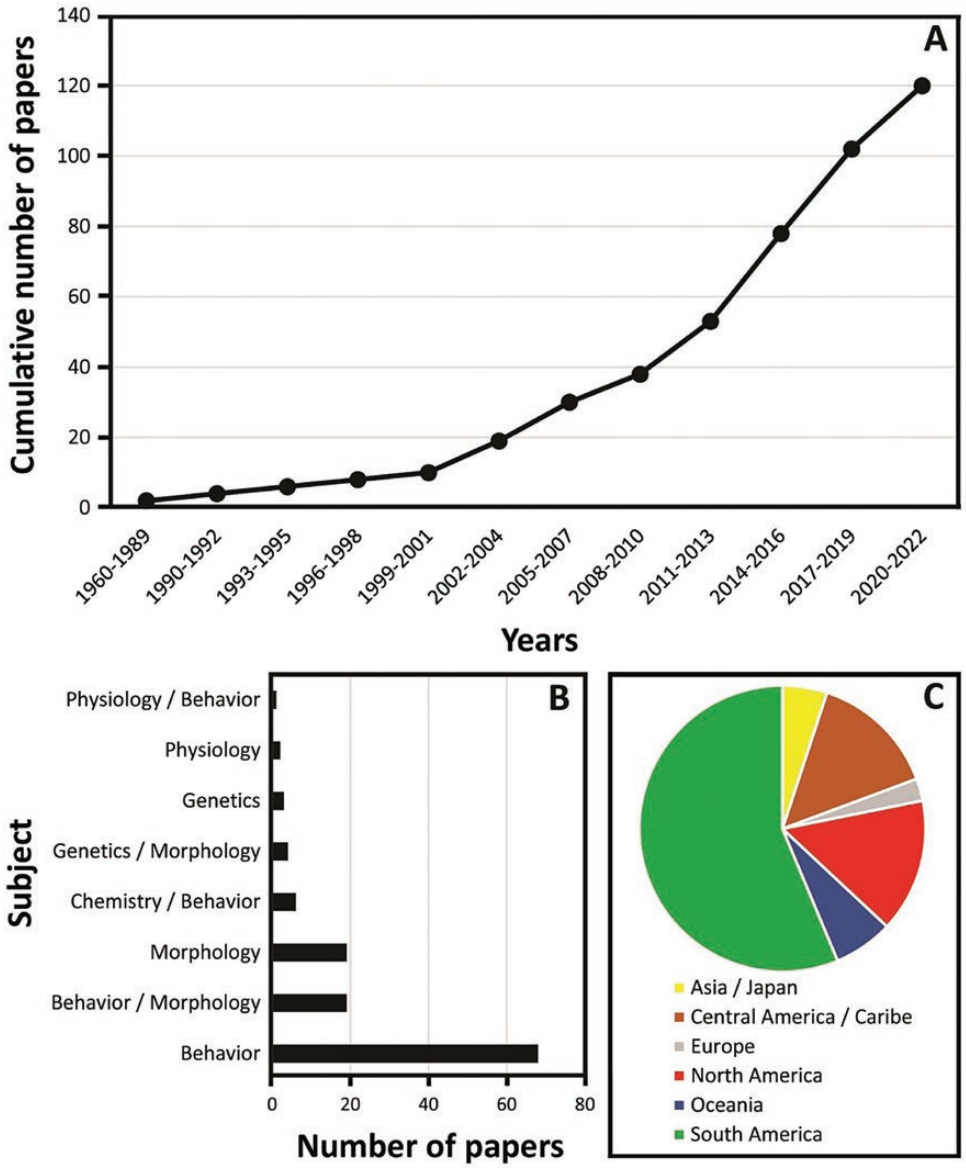

Figure 1 Results of a literature search conducted in the *Web of Science* database using the following combination of keywords: [(Opiliones or harvestm*) and (reproduct* or mating or copula* or sexual or oviposit* or egg* or "maternal care" or "paternal care")]. This search returned 266 results on 5 July 2022, from which 122 were directly related to the subject of this review. (A) Cumulative number of papers on reproductive biology of harvestmen according to the results of the literature search. Note that after the publication of the book *Harvestmen: The Biology of Opiliones* in 2007 there is a marked increase in the number of papers on reproductive biology. (B) The papers on reproductive biology were classified according to the main subject treated in the study (some papers focused on more than 1 subject). The subjects more intensively studied were behavior, morphology, and a combination of these 2 subjects. (C) The papers were also classified according to the region where the study was conducted. Most of the papers on reproductive biology were conducted in South America, followed by North and Central America (including the Caribbean).

reproductive behaviors and provide an overview of what we currently know about the reproductive biology of harvestmen.

Precopulatory Phase

Mating or no mating

The great majority of harvestman species reproduce sexually, but there are a few exceptions. Some species belonging to the suborders Eupnoi, Dyspnoi, and Laniatores (see phylogeny in Figure 2) reproduce via parthenogenesis, a form of asexual reproduction in which the development of embryos occurs without fertilization by sperm (Tsurusaki 1986; Table 1). Parthenogenesis in harvestmen may be obligate or facultative. Several species of *Acropsopilio* (Dyspnoi: Acropsopilionidae) and *Caddo* (Eupnoi: Caddidae) appear to reproduce mainly via parthenogenesis because males are extremely rare in field samples throughout the entire range of the species (Table 1). In *Megabunus lesserti* (Eupnoi: Phalangiidae) from the northeastern Alps, there are both unisexual (obligately parthenogenetic) and bisexual populations. Bisexuals occur in a small area that was not covered by ice during the last glaciation, whereas unisexuals occur in postglacially recolonized areas (Muster et al. 2005; Wachter et al. 2016). A similar case of geographical parthenogenesis has also been reported for 2 Japanese species, *Leiobunum globosum* and *L. manubriatum* (Eupnoi: Sclerosomatidae), which are the best studied cases of parthenogenesis in harvestmen. Unmated females of both species lay eggs that develop and hatch normally, although males

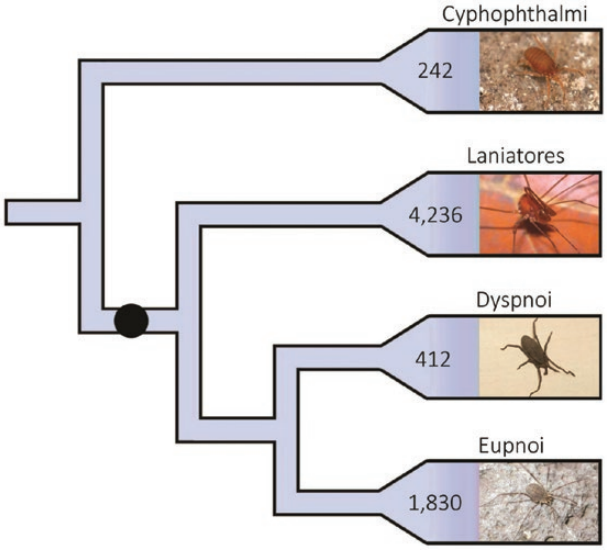

Figure 2 Internal phylogeny of the order Opiliones showing the 4 living suborders, and the clade Phalangida (indicated with a black dot). The topology follows Fernández et al. (2017), which is the most recent phylogeny of the order Opiliones. The numbers inside the branches indicate the number of species in each suborder according to Kury et al. (2021), which maintain an updated count of harvestman diversity. Cyphophthalmi: photo by Marshal Hedin (Wikipedia Commons); Laniatores: photo by Glauco Machado; Dyspnoi: photo by Dick Belgers (Wikipedia Commons); Eupnoi: photo by Glauco Machado.

also occur, indicating sexual reproduction is still maintained (Tsurusaki 1986). Both species have south-to-north and altitudinal clines of sex ratio, with males being rarer in northern and higher populations, respectively (Tsurusaki 1986; Burns et al. 2018).

As for most arthropods (Jaron et al. 2021; Burke and Bonduriansky 2022), the evolution of asexuality in harvestmen is hypothesized to be due to breakdowns in oogenesis, producing an automictic pathway that maintains recombination in affected lineages. The conditions that favor generation of primarily asexual populations, at least for *L. globosum* and *L. manubriatum*, are likely to be low vagility and stable, although heterogeneous, environmental conditions (Tsurusaki 1986; see also Burke and Bonduriansky 2019). Populations in marginal environments are typically female-biased (Burns et al. 2018). Although the sexes are equally capable of incremental migration, we hypothesize that the ability to reproduce asexually allows populations of females to be established and maintained at low densities, despite the disadvantages of asexual reproduction. In core habitats, sexual conflict may be responsible for maintaining males within populations via antagonistic mating (Brown et al. 2021). We do not know, however, if these mechanisms also apply to other parthenogenetic harvestman species. More studies on asexual species are certainly necessary to understand the evolutionary advantages and the repeated evolution of parthenogenesis in harvestmen (Table 1).

Who mates with whom?

The term "mating system" refers to how many mates each sex may have during a breeding season or the entire life (Emlen and Oring 1977). All the sexually reproducing species of harvestmen are probably polygynandrous (Buzatto et al. 2013; Machado et al. 2015), meaning both sexes may have multiple mates. A key aspect of mating systems is mate monopolization, which occurs when individuals of one sex (usually males) monopolize access to individuals of the other sex (Emlen and Oring 1977). In some polygynous mating systems, males can defend resources used by females, such as oviposition sites (see topic *Where to Lay Eggs?*). One single male can have exclusive access to several females, characterizing resource defense polygyny (Emlen and Oring 1977). Resource defense polygyny usually involves fights between males for resource possession, and males typically bear specialized fighting-related traits. Males of many harvestman species of Laniatores have spines on their legs and pedipalps, elongated appendages, or hypertrophied chelicerae that are used as weapons or threat devices (*sensu* Eberhard et al. 2018) in fights for the possession of the preferred oviposition sites (Buzatto and Machado 2014; Figure 3A). Females visit the territory defended by a male, mate with him, and have access to the oviposition site. These females usually stay inside the male's territory, forming harems (e.g., Buzatto and Machado 2008; Zatz et al. 2011; Palaoro et al. 2022; Figure 3B).

When females are monopolized by a few large males bearing well-developed fighting-related traits, one may think that small males bearing poorly developed traits do not have access to mates. This is not the case, however. In many species, small males bearing reduced or completely absent fighting-related traits exhibit so-called alternative reproductive tactics. The reproductive tactics are referred to as "alternative" because small males do not engage in agonistic interactions for resource monopolization. Instead, they sneak copulations, act as satellites, or even mimic females to invade territories or harems guarded by large males (examples in Oliveira et al. 2008). Alternative reproductive tactics are widespread among the Laniatores, but also occur in some species of Eupnoi (Buzatto and Machado 2014). Alternative reproductive tactics are usually coupled with male polymorphism, i.e., the presence of discrete male morphs in the same population that can be recognized by differences in body size and/or size of fighting-related traits (Buzatto and Machado 2008; Zatz et al. 2011; Painting et al. 2015; Solano-Brenes et al. 2018; Powell et al. 2020; Palaoro et al. 2022). In *Serracutisoma proximum* (Laniatores: Gonyleptidae), for instance, there are 2 male morphs that differ in the length of the second pair of legs (Buzatto et al. 2011). Large males with a long second pair of legs (i.e., majors) fight for the possession of oviposition sites on the vegetation using their elongated legs as threat devices (Figure 3A). Small males with a short second pair of legs (i.e., minors) do not fight, and their reproductive tactic relies on invading the harems of large males and sneaking copulation with egg-tending females (Buzatto et al. 2011; Figure 3B). In *Forsteropsalis pureora* and *Pantopsalis cheliferoides* (Eupnoi: Neopilionidae), there are 3 male morphs easily recognized by the size and shape of their chelicerae: alpha males are large-bodied with short but robust chelicerae, beta males are large-bodied with long, slender chelicerae, and gamma males are small-bodied with short, delicate chelicerae (Painting et al. 2015; Powell et al. 2020; Figure 4). Whereas alpha and beta males probably rely on territory defense, gamma males probably act as sneakers.

Given that the reproductive tactics of the male morphs are markedly different, some studies have explored the costs associated to territory defense and scramble competition in harvestmen. Territory defense necessarily involves agonistic interactions, which may increase the risk of injuries to the

Table 1 List of parthenogenetic harvestman species, with information on the locality and type of parthenogenesis (*obligatory*: when all populations are parthenogenetic; *geographic*: when only some populations are parthenogenetic)

Suborder (family)	Species (valid name)	Species (as in the publication)	Locality	Type of thelytoky	Sources
Dyspnoi (Acropsopilionidae)	*Acropsopilio boopis*	*Acropsopilio boopis*	Japan, USA	Obligatory*,**	Shear (1974) and Suzuki (1976)
	Acropsopilio chilensis	*Acropsopilio chilensis*	Chile	Obligatory*	Maury et al. (1996)
	Acropsopilio chomulae	*Acropsopilio chomulae*	Mexico	Obligatory*,**	Shear (2004)
	Acropsopilio neozealandiae	*Acropsopilio neozealandiae*	New Zealand	Obligatory*	McCartney et al. (2007)
	Acropsopilio venezuelae	*Acropsopilio venezuelae*	Venezuela	Obligatory*	González-Sponga (1992)
Dyspnoi (Sabaconidae)	*Sabacon* sp.	*Sabacon* sp.	Western USA	Obligatory*	Cokendolpher, pers. comm. in Tsurusaki (1986)
Dyspnoi (Taracidae)	*Crosbycus dasycnemus*	*Crosbycus dasycnemus*	Japan, USA	Obligatory*	Suzuki et al. (1977)
Eupnoi (Caddidae)	*Caddo agilis*	*Caddo agilis*	Japan, USA	Obligatory*	Gruber (1974), Suzuki and Tsurusaki (1983), Shear (1974), Suzuki (1972, 1976) and Shultz and Regier (2009)
	Caddo pepperella	*Caddo pepperella*	Japan, USA	Obligatory*	Shear (1974,) Suzuki (1976) and Shultz and Regier (2009)
Eupnoi (Phalangiidae)	*Megabunus diadema*	*Megabunus diadema*	UK, Iceland, Western Europe	Obligatory*	Phillipson (1959) and Martens (1978)
	Megabunus lesserti	*Megabunus lesserti*	Central Europe	Geographic	Martens (1978) and Muster et al. (2005)
	Platybunus pinetorum	*Platybunus pinetorum*	Central Europe	Geographic	Martens (1978)
Eupnoi (Sclerosomatidae)	*Leiobunum globosum*	*Leiobunum globosum*	Japan	Geographic	Tsurusaki (1986)
	Leiobunum manubriatum	*Leiobunum manubriatum*	Japan	Geographic	Tsurusaki (1986)
Laniatores (Assamiidae)	*Bandona boninensis*	*Bandona boninensis*	Japan	Obligatory*	Suzuki (1978)
Laniatores (Cladonychiidae)	*Briggsus bilobatus*	*Pentanychus bilobatus*	USA	Geographic	Briggs (1971)
	Isolachus spinosus	*Isolachus spinosus*	USA	Obligatory*	Briggs (1971)
Laniatores (Petrobunidae)	*Proscotolemon sauteri sauteri*	*Proscotolemon sauteri sauteri*	Japan	Obligatory*	S. Suzuki, pers. comm. in Tsurusaki (1986)

This list is based on Table 6 by Tsurusaki (1986) with some additions.
*Indicates that males are unknown or extremely rare in natural populations.
**Indicates absence of spermathecae in the ovipositor, which suggests the species is parthenogenetic.

males. In turn, scrambling involves high investment in mate searching, which may increase the risk of encountering predators. A comparison of the frequency of amputated legs—an injury imposed by a rival during agonistic interactions for territory defense—showed no difference between majors (56 of 459 males) and minors (14 of 83 males) of the harvestman *Longiperna concolor* (Laniatores: Gonyleptidae) (G. Machado unpub. data). Perhaps, minors are attacked and injured by majors during attempted territory invasion, which may explain their high incidence of leg amputation. Moreover, a long-term mark-recapture study with *S. proximum* showed that the survival rates do not differ between majors and minors (Buzatto et al. 2011), indicating that both morphs are under a similar mortality pressure imposed by natural enemies, such as predators and parasitoids. Finally, Powell et al. (2021) used leg autotomy—a common defensive behavior in Eupnoi—as a proxy of predation intensity and compared the frequency of leg loss between males that adopt a fighting tactic (alphas and betas) and males that adopt a scrambling tactic (gammas) in *F. pureora*. They found that the frequency of leg loss does not differ between males adopting different reproductive tactics, reinforcing the notion that the morphs are subject to similar predation intensity. Taken together, these results refute the hypothesis that the male morphs in harvestmen face different costs in terms of injury and mortality.

When mate monopolization is not possible, it is common that males search for females and both sexes mate multiple times. This form of polygynandry is called scramble

Figure 3 Resource defense mating system of the neotropical harvestman *Serracutisoma proximum* (Laniatores: Gonyleptidae). (A) 2 males fighting on the vegetation for the possession of a reproductive territory where females lay eggs (photo by Bruno A. Buzatto). During the fights, males hit each other with their elongated second pair of legs (arrows), which are much longer than those of females. (B) Harem containing 3 egg-tending females (white arrows) on the undersurface of the leaves (photo by Glauco Machado). The females are regularly inspected by the territorial male (black arrow), which prevents the approach of small males with short second pair of legs. These small males do not fight for territory possession, but rather invade the territories defended by large males and try to sneak copulations with the egg-tending females, which retain some eggs in their reproductive tract after mating with the territorial male.

competition, and it is probably the most common form of mate acquisition among arthropods (Herberstein et al. 2017). In harvestmen, scramble competition is possibly the ancestral state, being widespread among Eupnoi, Dyspnoi, and probably Cyphophthalmi (Buzatto et al. 2013). Females in these 3 suborders 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; see topic *Where to Lay Eggs?*). Although there are some records of male–male fights for the possession of receptive females in species showing scramble competition (e.g., Pabst 1953; Parisot 1962; Edgar 1971; Macías-Ordónez 1997), males rarely exhibit exaggerated fighting-related traits (Machado et al. 2016) and there is no evidence of alternative reproductive tactics (Buzatto and Machado 2014).

Precopulatory contact and nuptial gifts

Precopulatory interactions in many arachnids are dangerous because females may attack and cannibalize approaching males before copulation (Thomas and Zeh 1984; Elgar 1992). In spiders, for instance, long-distance, elaborate, highly stereotyped, and species-specific visual or vibratory displays are usually employed to announce both the identity and the "intention" of approaching males (Robinson 1982). In harvestmen, however, precopulatory cannibalism has never been recorded, and regardless of suborder, there is no evidence of elaborated or stereotyped precopulatory courtship by males (Machado and Macías-Ordóñez 2007; Machado et al. 2015). In most species, a male is probably unable to detect a female until direct physical contact is established between them (Fowler-Finn et al. 2014, 2019). However, *Leiobunum ventricosum* (Eupnoi: Sclerosomatidae) males have been observed moving fast toward a female prior to making physical contact with her, suggesting short-distance perception (Fowler-Finn et al. 2014, 2019). Once a male and a female detect each other, precopulatory interactions are usually brief and involve tactile and close-range chemical stimuli.

After initial contact, the couple generally adopts a face-to-face position, with the male using his pedipalps to grasp the female (Figure 5A). This behavior has been reported for many species of Eupnoi and Laniatores (Machado et al. 2015). Detailed morphological and behavioral studies of mating interactions in North American species of *Leiobunum* and *Hadrobunus* (Eupnoi: Sclerosomatidae) have found a gradient of sexual antagonism in the precopulatory phase (Fowler-Finn et al. 2014, 2018, 2019; Burns et al. 2015; Burns and Shultz 2016). Males of species showing high-sexual antagonism have a long and stiff penis capable of applying great biomechanical force on the female genital operculum. Females, in turn, have sclerotized pregenital barriers that are capable of blocking forced mating attempts. Moreover, the pedipalps of the males are long and robust (Figure 5A), sometimes bearing structures used to grasp the female and hold her fast during intromission. In species in which sexual antagonism is low, males have a more flexible penis and females lack pregenital barriers. Moreover, the pedipalps of the males are gracile and sexually monomorphic (Figure 5A). Finally, females of most species feed on secretions produced in glands located on the everted penis (Figure 5A). These secretions are composed of water and amino acids, which suggests that the nuptial gift is nutritious (Kahn et al. 2018). However, only males of species with low-sexual antagonism have specialized sacs on the penis that facilitate the delivery of the nuptial gift to the female mouth prior to intromission. These specialized sacs have been secondarily lost in species with high-sexual antagonism (Burns et al. 2013).

In Laniatores, females also seem to feed on secretions produced in glands located on the everted penis during pedipalpal grasping (Macías-Ordóñez et al. 2010), but no formal description of these putative glands has been made. No pedipalpal grasping has been reported for species of Dyspnoi. This difference can be partially explained by the fact that some species of this suborder, such as representatives of Trogulidae, mate in a belly-to-belly position, with male and female facing in opposite directions (Pabst 1953). Although there is no record of transference of nuptial gifts via penis in Dyspnoi, males of *Ischyropsalis* (Ischyropsalididae) and *Paranemastoma* (Nemastomatidae) release secretions in a pair of glands located dorsally on the first segment of their chelicerae, which are offered to the female before intromission (Martens 1969; Meijer 1972; Figure 5B). This is an interesting example of convergent evolution of nuptial gifts in harvestmen.

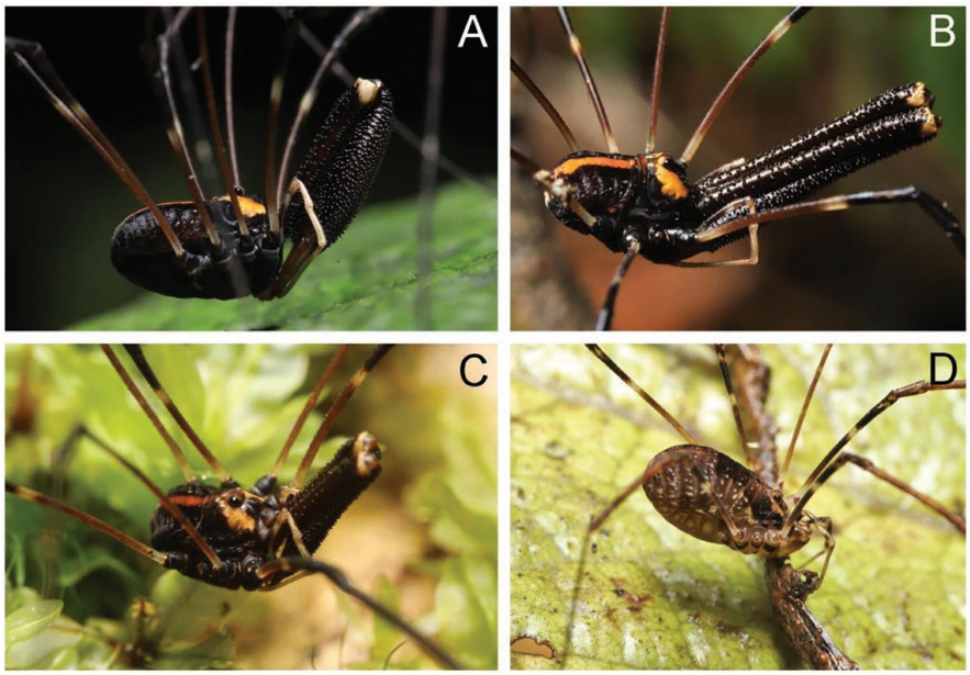

Figure 4 Sexual dimorphism and intrasexual polymorphism in the New Zealand harvestman *Forsteropsalis pureora* (Eupnoi: Neopilionidae). (A) Alpha male with large body size and short but robust chelicerae. (B) Beta male with large body size and long, slender chelicerae. (C) Gamma male with small body size and short, delicate chelicerae. (D) Female with body size similar to those of gamma males, and very small chelicerae when compared with males of the three morphs. Photos by Erin C. Powell.

Copulatory Phase

More touches and gifts

The ancestral form of sperm transfer in harvestmen is probably the transference of a spermatophore from the male to the female using a spermatopositor organ (van der Hammen 1985). The spermatopositor is found exclusively in Cyphophthalmi, which is the sister group to all other living Opiliones suborders (Figure 2). Although there is no behavioral information on how the spermatophore is transferred, the shape of the spermatopositor, the way the spermatophores have been found attached to the female genital operculum, and anecdotal observations of pre-copulatory interactions suggest direct participation of the male during sperm transfer (Karaman 2005; Schwendinger and Giribet 2005). Thus, it is reasonable to assume that all harvestman species require direct male–female contact to transfer sperm.

In species belonging to the clade Phalangida, which comprises Eupnoi, Dyspnoi, and Laniatores (Figure 2), males and females actively interact during copulation by touching, rubbing, tapping, grasping, pushing, and pulling each other in many ways with legs, pedipalps, and chelicerae (e.g., Immel 1954; Machado and Oliveira 1998; Willemart et al. 2006; Nazareth and Machado 2009; Fowler-Finn et al. 2014, 2018, 2019; Stanley et al. in press). Intense tactile stimulation, performed mainly by males, is probably a form of copulatory courtship (Machado and Macías-Ordóñez 2007; Machado et al. 2015). During intromission, females of some species of *Leiobunum* (Eupnoi: Sclerosomatidae) also feed on secretions produced in glands located in the penis (Wijnhoven 2011; Burns et al. 2013; Fowler-Finn et al. 2014, 2018, 2019; Figure 5A). Thus, nuptial gifts are offered both before and during copulation in this genus (Kahn et al. 2018). Interestingly, a recent study with *L. vittatum* has shown that when males and females are water deprived, copulation duration is greatly reduced (Sasson et al. 2020). This finding suggests that the hydration status of the individuals has an important role in how long intromission will last and consequently in how much sperm will be transferred to the female. Whether hydration status affects the quantity and/or quality of the nuptial gift is an open question. Male size also affects copulatory interactions in *L. vittatum*, as intromission duration is longer for smaller males (Fowler-Finn et al. 2018). The meaning of this pattern is not well understood, but the authors argue that, if smaller males are less attractive and have lower chances of mating, they should invest more in sperm transfer to increase their fertilization success when they are accepted by a female.

Genital interactions

The morphology of the intromittent male genitalia in harvestmen is incredibly diverse (Macías-Ordóñez et al. 2010; Figure 6). In all species of the clade Phalangida (Figure 2), the penis is divided into 2 main parts: the *pars basalis*, which corresponds to most of the long shaft, or truncus, and the *pars distalis*, which contains the distal end of the truncus and the terminal or subterminal glans. The *pars basalis* contains the sacs that proffer secretions during precopulatory and copulatory interactions (Burns et al. 2013). The *pars distalis*, in turn, interacts with the ovipositor (Figure 6). The glans is a highly variable structure that contains the stylus, from which sperm is released inside the female reproductive tract (Figure 6). In Eupnoi and Dyspnoi, the *pars distalis* is composed almost exclusively of a morphologically simple glans with an apical stylus, with the glans being only slightly differentiated from the truncus (Figure 6A,B). The glans in Laniatores is morphologically more complex, clearly differentiated from the

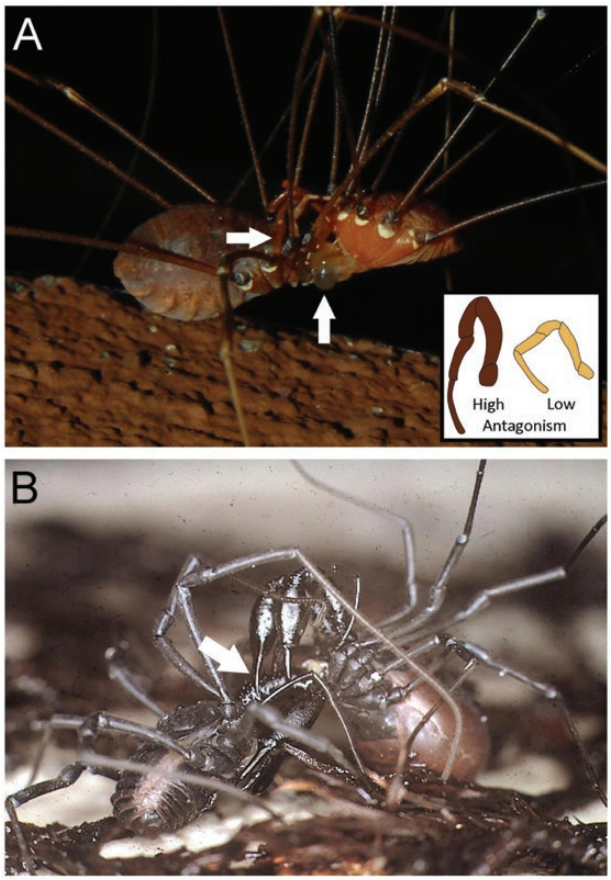

Figure 5 Nuptial gifts in 2 harvestman species. (A) Mating pair of *Leiobunum vittatum* (Eupnoi: Sclerosomatidae) during intromission: male on the right and female on the left (photo by Jerry Armstrong). The male's pedipalps are grasping the base of the female's second pair of legs (horizontal arrow). Sexual antagonism is high in this species and male's pedipalps are longer and more robust than in species in which sexual is low (inset). Note that the female's mouthparts are in contact with the base of the penis, probably feeding on glandular secretions (vertical arrow). (B) Mating pair of *Ischyropsalis hellwigi* (Dyspnoi: Ischyropsalididae) during precopulatory interactions: female on the right and male on the left (photo by Jochen Martens; original source: Martens, 1969). Note that the female's chelicerae are in contact with the base of the male's chelicerae (arrow), where a glandular secretion is released.

truncus, and contains several sclerites and macrosetae that vary widely among families (Figure 6C,D).

The morphological complexity of male genitalia is usually related to postcopulatory processes, such as sperm competition and cryptic female choice (Simmons 2014). If a female copulates with 2 or more males, the male that better stimulates her reproductive tract with his genitalia during copulation may have a higher chance of fertilizing the eggs because the female has morphological and physiological traits that allow her to select the sperm of the best partner (Eberhard 2015). Among arachnids, genital interactions have been intensively studied in spiders, and there is evidence that male genital stimulation may: 1) increase intromission duration, allowing the transference of more sperm; 2) increase the chance of a female dump sperm of previous males, decreasing sperm competition; and 3) induce female participation in forming copulatory plugs, which prevents further copulations (examples in Aisenberg et al. 2015 and Calbacho-Rosa and Peretti 2015). Despite the tremendous morphological diversity of male genitalia in harvestmen, there is scarce information on genital interactions (Macías-Ordóñez et al. 2010). We know, however, that the morphology of the ovipositor in Eupnoi, Dyspnoi, and Laniatores shows striking differences (Martens et al. 1981; Townsend et al. 2015). These differences will determine the type of genital interactions, the degree of stimulation that may be provided by males, and consequently the role of postcopulatory processes, such as sperm competition and cryptic female choice, in influencing paternity.

In Eupnoi, the needle-like stylus distal to the glans enters the female seminal receptacles, wherein sperm is released (Figure 6A). With the stylus inserted in the seminal receptacles, the basal portion of the glans possibly contacts a region with abundant sensilla at the tip of the ovipositor. This suggests that the glans stimulates the sensilla used by the females to probe oviposition sites (Machado and Macías-Ordóñez 2007). The penis in Dyspnoi is similar to that of Eupnoi (Figure 6A,B), but the ovipositor is very different, being shorter and with smaller seminal receptacles (Martens et al. 1981). The stylus does not fit the seminal receptacles and the sperm is probably released in the lumen of the ovipositor. Thus, the female possibly has the control over transportation of the sperm for storage. Another difference in Dyspnoi is that the ovipositor has few sensilla and is probably less sensitive to the stimulation of the penis (Machado and Macías-Ordóñez 2007).

The morphologically complex penis in Laniatores (Figure 6C, D) possibly exerts 3 main functions: 1) to fasten the *par distalis* at the distal end of the ovipositor, where the seminal receptacles are located; 2) to promote intromission in the ovipositor; and 3) to open the X-shaped vaginal lumen in order to expose the stylus, which will release sperm (Macías-Ordóñez et al. 2010). As in Dyspnoi, the female possibly controls transport of sperm to the seminal receptacles, presenting the possibility of cryptic female choice to occur. Finally, the ovipositor in Laniatores shows even fewer sensilla than the other suborders, and the penis possess a unique set of highly variable and complex structures (e.g., macrosetae) that are supposed to stimulate these sensilla or some internal parts of the female reproductive tract (Macías-Ordóñez et al. 2010).

Male strategies for enhancing female stimulation and biasing insemination via cryptic female choice may have coevolved with female strategies that restrict accessibility to the seminal receptacles by the means of a narrow vaginal lumen, loss of sensitivity, promotion of sperm competition, and even sperm ejection (Macías-Ordóñez et al. 2010; see topic *Sperm Competition*). Given the interspecific variation in both penis and ovipositor morphology (Martens et al. 1981; Macías-Ordóñez et al. 2010; Townsend et al. 2015 and references therein), harvestmen offer fertile ground to test hypotheses about genital diversification using a comparative approach. Moreover, given the relatively large size of male genitalia, it would be possible to perform studies of phenotypic engineering, in which microscale laser surgery is used to experimentally manipulate genital morphology (e.g., Hotzy et al. 2012).

In a detailed morphological study, Pérez-González and Werneck (2018) described for the first time the mechanical eversion of the glans and discussed the role of different penial structures during genital coupling in harvestmen. The study species was *Triaenonychoides cekalovici* (Laniatores: Triaenonychidae), in which penis eversion is performed via a muscular system. This type of penis eversion is characteristic of Eupnoi and Dyspnoi, as well as of the superfamilies

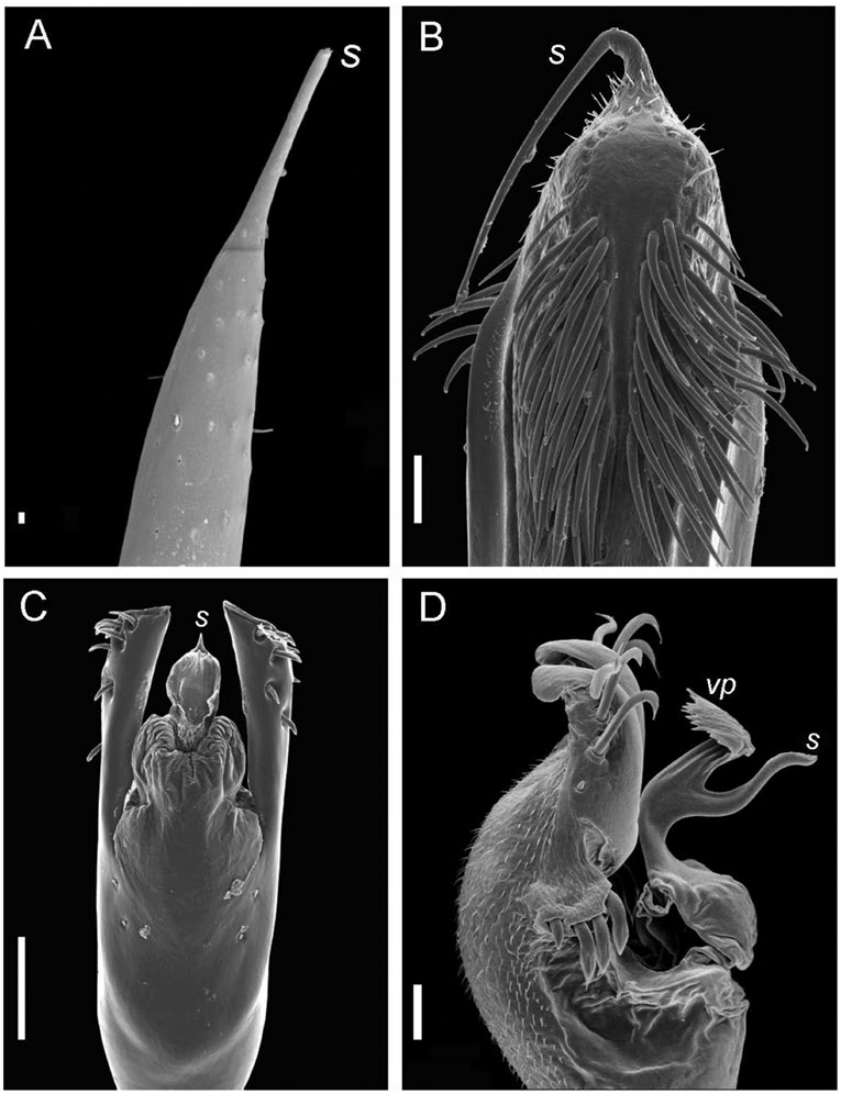

Figure 6 Male genital morphology in harvestmen. (A) Dorsal view of the glans of *Jussara flamengo* (Eupnoi: Sclerosomatidae), a representative of the suborder Eupnoi (photo by Ricardo Pinto-da-Rocha). Scale bar = 3 µm. (B) Dorsal view of the glans of *Ischyropsalis robusta* (Ischyropsalididae), a representative of the suborder Dyspnoi (photo by Adriano B. Kury). Scale bar = 50 µm. (C) Dorsal view of the glans of *Orobunus quadrispinosus* (Podoctidae), a representative of the suborder Laniatores (photo by Adriano B. Kury). Scale bar = 100 µm. (D) Lateral view of the glans of *Hernandaria unus* (Gonyleptidae), a representative of the suborder Laniatores (photo by Ricardo Pinto-da-Rocha). Scale bar = 20 µm. In all photos, *s* indicates the *stylus*, which contains the ejaculatory ductus. In (D), *vp* indicates the ventral process, which may be responsible for removing previous sperm from the female reproductive tract.

Travunioidea and Triaenonychoidea (Laniatores), and contrasts with the clade Grassatores (Laniatores), in which penis eversion is hydraulic (Macías-Ordóñez et al. 2010). The contraction of the muscle connected to the base of the ventral plate (a sclerotized structure on the *pars distalis*) triggers the eversion of the *capsula interna* where the stylus and other genital sclerites are located. The eversion of the *capsula interna* is probably necessary for positioning the stylus closer to the female seminal receptacles. Considering that harvestmen have immobile, aflagellate spermatozoa (see topic *Sperm Competition*), releasing sperm closer to the seminal receptacles can be advantageous for males. Although these findings represent an important first step in our understanding of the genital interactions in harvestmen, we need to explore how general they are, and how genital coupling occurs in species in which penis eversion occurs via a hydraulic system.

Sperm competition

Whenever a female mate with 2 or more males, the sperm of these males may compete for the access to the ovocytes in a process called sperm competition (Parker 1970). Sperm competition is an important selective force driving the evolution of several male traits, such as penis morphology, testes size, and sperm number, viability, and velocity (Simmons 2001). As mentioned in the topic *Who Mates with Whom?*, females of many harvestman species mate multiple times, and thus sperm competition is probably widespread in the order. Indirect evidence of the importance of sperm competition in harvestmen is the presence of mating plugs, recently described for 6 species of Cosmetidae, Gonyleptidae, Metasarcidae, and Kimulidae (Laniatores). In each of these species, masses of amorphous, gel-like material were found obstructing the distal openings of the ovipositors (Townsend et al. 2019). Mating plugs are widespread in vertebrates

and invertebrates and have the main function of reducing or preventing sperm competition by inhibiting females from mating with multiple males for a period of time (e.g., Shine et al. 2000; Uhl et al. 2010). Some features of the male genital morphology also seem to be linked to sperm competition in harvestmen. In Laniatores, a specific structure of the glans known as the ventral process (Figure 6D) is suggested to be used to remove sperm from previous mates (Macías-Ordóñez et al. 2010). Sperm removal has already been reported for other highly polygynandrous arthropod groups, such as odonates (Waage 1979), orthopterans (von Helversen and von Helverse 1991), beetles (Haubruge et al. 1999), earwigs (Kamimura 2005), and spiders (Calbacho-Rosa et al. 2013). Therefore, it would not be surprising to find this behavior in harvestmen.

One of the many unique reproductive traits of harvestmen is the presence of immobile, aflagellate spermatozoa (Morrow 2004). Lack of flagelliform sperm cells has important implications for cryptic female choice: sperm movement, if any, is probably controlled by the female inside her reproductive tract (Macías-Ordóñez et al. 2010). Once inside the seminal receptacles, the only movement performed by the sperm is probably restricted to exiting. This may happen either by the flushing action of new ejaculates (a form of sperm removal) or by female control, deforming the seminal receptacles by contracting the ovipositor muscles (Martens et al. 1981). Females may guide syngamy by activating the seminal receptacles as mature ovocytes travel through the ovipositor and reach the tip of the ovipositor where fertilization occurs. Alternatively, females may eject sperm in the absence of any fertilizable egg as a form of spermatic rejection, which can be regarded as cryptic female choice (Macías-Ordóñez et al. 2010). Although sperm ejection has never been formally demonstrated in harvestmen, the fact that females in many Laniatores and Eupnoi manipulate the tip of the ovipositor with their mouthparts after copulation suggests that they may be feeding on ejected sperm. In *Pachyloides thorellii* (Laniatores: Gonyleptidae), females evert the ovipositor after copulation until its distal extreme contacts the mouthparts. The tip of the ovipositor can also be scraped with the claws of the pedipalps, which are then taken to the mouthparts. This behavior can be repeated several times and researchers speculate that females may be dumping and feeding on sperm (Stanley et al. in press).

Sperm immobility also has important implications for sperm competition. All model systems of sperm competition, such as fruit flies, beetles, rats, and humans, have motile spermatozoa, so that traits such as sperm velocity, ATP content, and resistance to oxidative stress play a key role in increasing fertilization success (Pizzari and Parker 2009). In harvestmen, however, sperm motility is useless because they are received and stored in the seminal receptacles at the tip of the ovipositor, and do not travel far inside the female reproductive tract (Machado and Macías-Ordóñez 2007). Moreover, given that females of some harvestman species can live several years as adults (Gnaspini 2007), males that produce sperm with high longevity and viability are expected to sire more eggs in a war of attrition with sperm of rival males stored in the female seminal receptacles. Finally, males can place more sperm inside the small female seminal receptacles if they lack flagella (Machado and Macías-Ordóñez 2007). All these hypotheses have never been tested and may provide insights on the evolution of sperm aflagellarity, which remains a poorly understood subject in sexual selection (reviewed in Morrow 2004).

Although pervasive in polyandrous species, sperm competition does not act equally in males of the same population. When there are alternative reproductive tactics, males that exhibit the nondominant tactic (i.e., those that sneak copulations) usually mate with females that have already mated with the males that exhibit the dominant tactic (i.e., those that defend territories). Assuming that territorial males are the first to copulate with virgin females, sneakers are expected to always face sperm competition (Parker 1990). Under this circumstance, sneakers should invest in traits that maximize their fertilization success, such as large testes size. Large testes increase the competitiveness of a male because they increase the quantity of sperm transferred to the female, and thus provide a numerical advantage (Parker 1990; but see Dougherty et al. 2022). Assuming that aflagellate sperm are less costly to produce (Morrow 2004), sneaker males may be able to invest in a larger number of spermatozoa to increase fertilization success. This hypothesis has been tested for the harvestman *Serracutiosma proximum* (Laniatores: Gonyleptidae), which has 2 male morphs exhibiting different mating tactics (see topic *Who Mates with Whom?*). Contrary to theoretical predictions, testes mass did not differ between male morphs (Munguía-Steyer et al. 2012). According to the authors, the high frequency of successful invasions by sneakers (Buzatto et al. 2011; Muniz and Machado 2015) and hence the high-sperm competition risk for both morphs may explain the similarity in gonadal investment between majors and minors. Alternatively, females may have full control of the fate of the sperm (see topic *Genital Interactions*) and a great investment in sperm count may not increase male competitiveness (for further discussion, see Kustra and Alonzo 2020).

Postcopulatory Phase

Guard your mating partner

After copulation, many harvestman species exhibit a behavior called mate guarding, wherein mating partners remain close for some time, minimizing female remating (Alcock 1994). In *Leiobunum* spp. (Eupnoi: Sclerosomatidae), the male guards the female wrapping one of her legs with his first pair of legs and following her as she selects potential oviposition sites with her ovipositor (Macías-Ordóñez 1997; Wijnhoven 2011; Fowler-Finn et al. 2014, 2018, 2019; Figure 7A). During mate guarding, males ignore other females and repel any male that approaches their mating partner (Macías-Ordóñez 1997, 2000; Wijnhoven 2011). In *L. vittatum* and *L. ventricosum*, the likelihood and duration of mate guarding are higher when females are larger and probably more fecund, suggesting that males adjust their postcopulatory behavior in response to female quality (Fowler-Finn et al. 2018). Besides excluding other male competitors, mate guarding in *L. ventricosum* may allow repeated copulations given that males often remate with the female after releasing her leg (Fowler-Finn et al. 2018).

In *Acutisoma longipes* (Laniatores: Gonyleptidae), the male remains close to the female while she oviposits, waving his second pair of legs over her and occasionally tapping her legs and dorsum. Mate guarding may last more than 1 day, during which the male often remates with the guarded female (Machado and Oliveira 1998). A similar behavior occurs in *Serracutisoma proximum* (Laniatores: Gonyleptidae), in which small males constantly invade the territory of large males to

sneak copulations (Figure 7B). Field observations show mate guarding is performed almost exclusively by large males (i.e., majors), and that this behavior is highly efficient in preventing sneak copulations (Buzatto et al. 2011). Another example of mate guarding occurs in species in which males care for eggs inside natural cavities. In these species, such as *Gonyleptes ater* and *Magnispina neptunus* (Laniatores: Gonyleptidae), males may block the nest entrance after copulation so that rival males are prevented from entering (Machado et al. 2004; Nazareth and Machado 2010). The behavior of blocking the nest entrance can have a double function: 1) to prevent females from mating with additional males, thus protecting paternity, and 2) to prevent females from leaving the nest and perhaps increasing the number of eggs they lay.

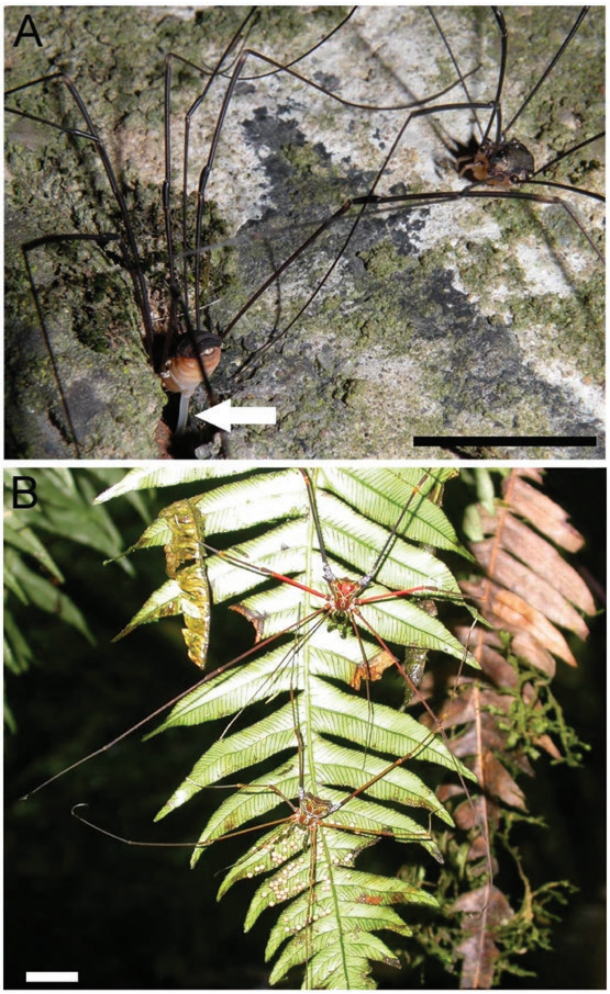

Figure 7 Mate guarding in harvestmen. (A) Male of *Leiobunum* sp. (Eupnoi: Sclerosomatidae) touching the female with the first pair of legs while she inserts the ovipositor (arrow) in a rock fissure to lay eggs (photo by Hay Wijnhoven). After mating, the male stays close to the female and this behavior prevents other males from approaching the females while she oviposits. (B) Male of *Serracutisoma proximum* (Laniatores: Gonyleptidae) with the second pair of legs extended frontwards guarding a female while she oviposits (photo by Bruno A. Buzatto). In this species, large males with a long second pair of legs are territorial and exhibit mate guarding whereas small males with a short second pair of legs invade the territories and try to sneak copulation with the egg-tending females. During mate guarding, some territorial males have been observed repelling the approach of sneaker males. Scale bars = 1 cm.

The main hypothesis to explain the occurrence of mate guarding is sperm competition, so that males exhibiting this behavior should fertilize relatively more eggs than males that abandon their mates after copulation (Alcock 1994). No experiment has been conducted with harvestmen to understand the function of mate guarding and estimate the fertilization success promoted by this behavior. If mate guarding in harvestmen has evolved or been maintained by sperm competition, the presence and duration of mate guarding may be related to the patterns of sperm use and storage between reproductive events (Machado et al. 2015). Basically, when the sperm of the last male that mated with a female has advantage in fertilizing the ovocytes, mate guarding may confer great benefits to this male in terms of sperm competition (Simmons 2001). The presence and duration of mate guarding may also be related to the chance of sperm removal by the female's subsequent mates (Machado et al. 2015). If the sperm of one male can be removed by subsequent males, mate guarding may prevent the female to mate with other males and thus protect the sperm of the male that is guarding her (Simmons 2001).

In North American species of the genus *Leiobunum*, such as *L. politum*, there are marked inter-populational differences in the likelihood and duration of mate guarding. In the Wisconsin population, mate-guarding occurred in 100% of the successful mating trials and lasted longer than in the Virginia population, where mate-guarding occurred in only 60% of the successful mating trials (Fowler-Finn et al. 2019). This species, therefore, offers the possibility to investigate what ecological conditions influence male investment in mate guarding. Another interesting species to explore questions related to mate guarding is *S. proximum* because adult sex ratio, density, and relative frequency of sneakers show great variation across populations (Munguía-Steyer et al. 2012). Thus, the costs and benefits of mate guarding should also vary among populations, leading to differences in the likelihood and duration of this behavior. Given the widespread occurrence of mate guarding in harvestmen, the integration of behavioral observations and paternity analyses make the group an ideal model system to investigate the fitness benefits of prolonged male–female association after sperm transfer.

Where to lay eggs?

The selection of oviposition sites has important implications for all species that lay eggs. A suitable site must provide good thermal and hydric conditions for the eggs, decrease their exposure to natural enemies, and increase the chances of the early-hatched young to feed (Bernardo 1996; Refsnider and Janzen 2010). In species with post-ovipositional parental care, the oviposition site must also provide appropriate conditions for the parents, because inadequate places may expose them to stressful and/or risky conditions (e.g., Morse 1985; Montgomerie and Weatherhead 1988). Thus, it is not surprising that females of oviparous arthropods carefully select the places where they lay their eggs (e.g., Bernays and Chapman 1994; Romero and Vasconcellos-Neto 2005). Harvestmen are not an exception and females of many species select oviposition sites.

Females of *Mitopus morio* (Eupnoi: Phalangiidae) from Germany lay their eggs inside small holes in the stems of shrubs bored by larvae of weevils and flies. The eggs laid during the summer hibernate inside the stems, where they can resist temperatures as low as –20 °C, and nymphs hatch in

the spring (Tischler 1967). The selection of this type of oviposition site is only possible because species of Eupnoi have a long and highly flexible ovipositor to insert their eggs inside small holes, cavities, and fissures in the soil, rocks, bark, and stems of both dead and live plants (Martens et al. 1981; Machado and Macías-Ordóñez 2007; Figure 7A). In turn, species of Dyspnoi have a short ovipositor that prevents the females from inserting their eggs deeply in protected places (Martens et al. 1981; Machado and Macías-Ordóñez 2007). Therefore, they select other types of oviposition sites where their eggs will be protected from harsh abiotic conditions and predators. Species of Trogulidae, for instance, feed exclusively on snails and females use the empty shells as their sole oviposition site (Pabst 1953). After oviposition, they block the entrance of the shell with a glandular secretion, keeping the eggs protected from predators inside the shell.

In Laniatores, females also have a short ovipositor and most species lay their eggs in exposed substrates. Some species, however, insert their eggs in shallow cavities or fissures in the bark or rocks (Machado and Macías-Ordóñez 2007). Among species that lay eggs in exposed substrates, some use the vegetation and there are clear examples of oviposition site selection. Females of *Bourguyia trochanteralis* (Laniatores: Gonyleptidae) lay their eggs almost exclusively inside the rosette formed by the curled leaves of the epiphytic bromeliad *Aechmea nudicaulis* (Machado and Oliveira 2002). Females select not only the plant species, but also exhibit precise discrimination of individuals of this plant. Bromeliads with longer rosettes are preferred possibly because they accumulate more water and maintain lower internal humidity variation than the external environment. Moreover, females avoid bromeliads with debris accumulation inside the rosettes possibly because debris fallen from the canopy can damage the eggs and block the rosette preventing the nymphs and egg-tending female from leaving the bromeliad after the caring period (Osses et al. 2008). These findings indicate that females can assess architectural features of the plants and select oviposition sites that promote adequate microhabitat for egg development and survival.

Another example of oviposition site selection occurs in *Quindina limbata* (Laniatores: Nomoclastidae), in which males build mud nests on fallen logs, most of which are not in direct contact with the ground. These nests are used by the females as the sole place to lay their eggs, and there is evidence suggesting that they evaluate nest integrity both before and after copulation with the nest owner (Rojas et al. 2019). Given that the species inhabits tropical forests, where intense rainfall destroys nearly 50% of the nests, males show a complex pattern of nest-site selection that responds to 3 proximate cues. First, males always build their nests in the bottom half of the fallen logs, where they are protected from the direct impact of raindrops. Second, males avoid the zones where the lateral drag force caused by flowing water, and thus, the risk of nest flooding, is high. Finally, males avoid the lowest part of the fallen log, where water saturation may kill the eggs. Therefore, nest-site selection in *Q. limbata* probably minimizes the risk of nest destruction, which imposes energetic costs to caring males because they must rebuild it. Nest-site selection may also maximize reproductive benefits because males with intact nests are more attractive to females. Finally, nest-site selection may increase offspring fitness, minimizing the risk of egg mortality associated with nest destruction and anoxia if nests are flooded during intense rainfall (Rojas et al. 2019, 2021).

Effects of oviposition site selection and climate on reproductive biology

The selection of oviposition sites as a possible consequence of a short ovipositor in Laniatores may have implications for other aspects of their reproductive biology. If the oviposition sites preferred by females are scarce or are clumped in the space, these sites can be profitably defended by males. It may explain why resource defense polygyny is more frequent in Laniatores than in other suborders with long ovipositor, in which this type of mating system is rare (Buzatto et al. 2013). It may also explain 2 other general patterns that are common in Laniatores, but rare in the remaining suborders. The first is a marked sexual dimorphism in body size and/or presence of fighting-related traits. Because large males tend to win fights for territory possession, intrasexual selection favors males with stronger or more efficient weapons, as well as males with larger threat devices (Eberhard et al. 2018). The second pattern is the high frequency of cases of male polymorphism, even when compared with other arachnid orders with a much larger number of species, such as spiders and mites (Buzatto and Machado 2014). In resource defense mating systems, small males with reduced or completely absent fighting-related traits usually rely on alternative mating tactics that rarely involve male–male contests (see topic *Who Mates with Whom?*). Whenever reproductive tactics with different phenotypic optima are successfully employed by males in a population, disruptive selection may lead to the evolution of male polymorphism (Gadgil 1972; Gross 1996).

There is one harvestman family that challenges the hypothesis presented above, the Neopilionidae (Eupnoi). Although females in this family have a long ovipositor and are able to hide their eggs, the mating system of some species seems to be a resource defense polygyny and male polymorphism has been formally reported for 2 of them (Painting et al. 2015; Powell et al. 2020). Unfortunately, the behavior of neopilionids is difficult to observe, both in the field and in the laboratory, which hampers a deeper comprehension of the evolution of their mating system. Regardless of the selective pressures that may have shaped the reproductive biology of neopilionids, the notion that the magnitude of sexual dimorphism and type of mating system depend only on the length of the ovipositor is an oversimplification. Other factors, such as climatic conditions should also be considered because they affect the time individuals have to reach adulthood and invest in mate acquisition traits. A short period of favorable climatic conditions constrains developmental time in annual species, leading to fast sexual maturity and marked reproductive synchrony, as occurs in many species of Eupnoi (Belozerov 2012). Thus, time-consuming activities, such as territorial defense, should be rare, and the most frequent mating system is expected to be scramble competition. In turn, when the period of favorable climatic conditions is long, reproduction is expected to be asynchronous, as already reported for some species of Laniatores (Machado et al. 2016). Moreover, assuming that gamete replenishing in harvestmen is faster for males than for females, populations should have a male-biased operational sex ratio (OSR). According to the theory, the combination of a male-biased OSR and the fact that males clearly benefit from multiple mates (i.e., a steep Bateman's Gradient) provides the necessary conditions for male investment in mate acquisition traits, such as fighting-related traits (Kokko et al. 2014). Thus, resource defense polygyny is expected to be a frequent-mating system (Machado et al. 2016).

The predictions presented above were tested in a macroecological study including nearly 100 harvestman species belonging to all suborders (Machado et al. 2016). Scramble competition is indeed associated with cold and dry climates where the breeding season is short, whereas resource defense polygyny is associated with warm and wet climates where the breeding season is long. In addition, the magnitude of sexual dimorphism is correlated with the type of mating system. In species with scramble competition, males are usually smaller than females and rarely have fighting-related traits, whereas in species with resource defense, males are usually larger than females and frequently have fighting-related traits (Machado et al. 2016). These findings provide additional explanation for the widespread occurrence of resource defense and male-biased sexual dimorphism in Laniatores, especially among tropical species.

Forms of parental care

Parental care occurs whenever one or both parents increase the survival of their offspring. Among arthropods, parental care can be divided into pre and postoviposition parental care. Preovipositional care occurs before egg laying and includes, for instance, oviposition site selection and provisioning of defensive structures into eggs (Smiseth et al. 2012). As mentioned in *Where to Lay Eggs?*, several species select oviposition sites, which is probably a generalized form of preovipositional care in the order. Another common form of preovipositional care in Dyspnoi and Laniatores is the presence of a highly hygroscopic mucus layer around eggs. After eggs are laid, the mucus layer absorbs water from the air, forming a thick jelly coat around them (Figure 8A–C). An experiment with *Neosadocus bufo* (Laniatores: Gonyleptidae) has shown that eggs surrounded by this jelly coat are more protected against predation by conspecifics and heterospecifics than eggs without the jelly coat (Chelini and Machado 2014). Because the mucus retains water, it is likely that the mucus also works as a buffer, preventing egg dehydration.

Postovipositional care occurs after egg laying and includes, for instance, egg coating, egg attendance, offspring attendance, and egg carrying (Smiseth et al. 2012). Egg coating occurs when females deposit chemicals or debris on their eggs after oviposition. Females of some species of *Leiobunum* (Eupnoi: Sclerosomatidae) rub their scent glands on the place where they have laid their eggs (Clawson 1988). The function of this behavior is not well understood, but the author hypothesizes that females are coating their eggs with defensive chemicals that are highly effective in repelling ants (Clawson 1988). However, considering that the chemicals released by harvestmen are highly volatile (Gnaspini and Hara 2007), we argue that the protective role (if any) they provide to the eggs is limited to a very short period. Another form of egg coating occurs in many species of Laniatores, in which females add debris to their eggs after oviposition. This behavior may camouflage the eggs against tactile-, chemically, and visually oriented predators (Machado and Raimundo 2001; Figure 8D). Egg coating with debris is the plesiomorphic form of parental care in Gonyleptidae (Caetano and Machado 2013) and probably in Laniatores as a whole.

Egg attendance occurs when parents remain close to the eggs at a fixed location after oviposition (Smiseth et al. 2012).

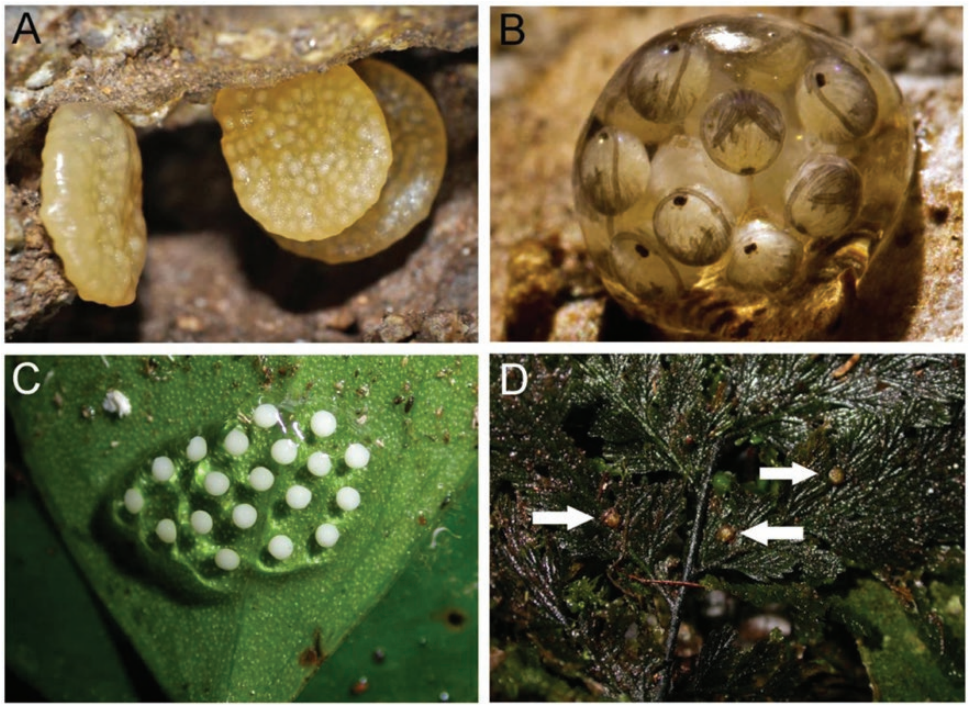

Figure 8 Egg coating in harvestmen. (A) Three clutches of *Ischyropsalis luteipes* (Dyspnoi: Ischyropsalididae) hanging from a cave wall in France (photo by Axel L. Schönhofer; source: https://wiki.arages.de/index.php?title=Ischyropsalis_luteipes). Each clutch, containing nearly 100 eggs, is surrounded by thick hygroscopic mucus coat. (B) Clutch of *Sabacon viscayanum* (Dyspnoi: Sabaconidae) with eggs embedded in a jelly coat in Wales (photo by Stephen Murray). Note the eyes and the legs of the embryos inside the eggs. (C) Clutch of *Iporangaia pustulosa* (Laniatores: Gonyleptidae) with eggs embedded in a jelly coat in Brazil (photo by Gustavo S. Requena). In this species, eggs are laid on the underside of leaves and are guarded by the males until the moment they hatch. (D) Eggs of *Promitobates ornatus* (Laniatores: Gonyleptidae) laid on a fern leaf in Brazil (photo by Bruno A. Buzatto). The eggs (arrows) are coated with debris, which probably camouflage them.

Table 2 List of harvestman species showing parental care, with information on the locality and caring sex

Family (Subfamily)	Species (valid name)	Species (as in the publication)	Locality	Caring sex	Sources
Assamiidae (Erecinae)	*Lepchana spinipalpis*	*Lepchana spinipalpis*	Nepal	Male	Martens (1993)
Cosmetidae (Cynortinae?)	*Cynorta bromeliacia*	*Cynorta bromeliacia*	Costa Rica	Male	Damron et al. (2021)
Cosmetidae (Meterginae)	*Erginulus clavotibialis*	*Erginulus clavotibialis*	Belize	Female	Goodnight and Goodnight (1976)
Cosmetidae (Metergininae?)	*Reimoserius* aff. *albipictus*	*Cosmetidae* sp.	Costa Rica	Male	Proud et al. (2011)
Cranaidae (Phareicranainae)	***Phalangodus briareos***	***Phalangodus briareos***	Colombia	Female	García-Hernández and Machado (2018a)
	Phareicranaus aff. *spinulata*	*Phareicranaus* aff. *spinulata*	Colombia	Female	García-Hernández and Machado (2018b)
	Phareicranaus calcarifer	*Santinezia serratotibialis*	Trinidad	Female	Machado and Warfel (2006)
	Phareicranaus manauara	*Phareicranaus manauara*	Brazil	Female	Colmenares and Tourinho (2014)
Gonyleptidae (Bourguyiinae)	***Bourguyia trochanteralis***	***Bourguyia hamata***	Brazil	Female	Machado and Oliveira (2002)
Gonyleptidae (Caelopyginae)	*Ampheres leucopheus*	*Ampheres leucopheus*	Brazil	Male	Hara et al. (2003)
Gonyleptidae (Cearininae)	*Liogonyleptoides tetracanthus*	*Liogonyleptoides tetracanthus*	Brazil	Female	Werneck et al. (2012)
	Parapachyloides fontanensis	*Apophysigerus fontanensis*	Argentina	Female	Canals (1936)
Gonyleptidae (Goniosomatinae)	***Acutisoma longipes***	***Goniosoma longipes***	Brazil	Female	Machado and Oliveira (1998)
	Goniosoma venustum	*Goniosoma geniculatum*	Brazil	Female	Machado (2002)
	Heteromitobates albiscriptum	***Goniosoma albiscriptum***	Brazil	Female	Willemart and Gnaspini (2004)
	Heteromitobates discolor	*Goniosoma discolor*	Brazil	Female	Machado (2002)
	Mitogoniella indistincta	*Goniosoma indistinctum*	Brazil	Female	Machado (2002)
	Mitogoniella mucuri	*Mitogoniella mucuri*	Brazil	Female	Ázara et al. (2013)
	Mitogoniella taquara	*Goniosoma* sp.	Brazil	Female	Machado et al. (2003)
	Mitogoniella unicornis	*Goniosoma* sp.n.1	Brazil	Female	Machado (2002)
	Serracutisoma catarina	*Goniosoma catarina*	Brazil	Female	Machado et al. (2001)
	Serracutisoma gnaspinii	*Goniosoma* aff. *proximum*	Brazil	Female	Machado (2002)
	Serracutisoma guaricana	*Undescribed goniosomatine from Guaricana*	Brazil	Female	Machado (2002)
	Serracutisoma molle	*Goniosoma* aff. *badium*	Brazil	Female	Pinto-da-Rocha (1993)
	Serracutisoma proximum	***Acutisoma proximum***	Brazil	Female	Ramires and Giaretta (1994) and Buzatto et al. (2007)
	Serracutisoma pseudovarium	*Goniosoma* sp.	Brazil	Female	Machado and Warfel (2006)
	Serracutisoma spelaeum	*Goniosoma spelaeum*	Brazil	Female	Gnaspini (1995)
Gonyleptidae (Gonyleptinae)	*Gonyleptes ater*	*Gonyleptes saprophilus*	Brazil	Male	Machado et al. (2004)
	Juticus sp.	*Neosadocus* sp.	Brazil	Male	Machado et al. (2004)
	Neosadocus bufo	***Neosadocus maximus***	Brazil	Female	Chelini and Machado (2012)

Table 2. Continued

Family (Subfamily)	Species (valid name)	Species (as in the publication)	Locality	Caring sex	Sources
Gonyleptidae (Heteropachylinae)	*Heteropachylus inexpectabilis*	*Chavesincola inexpectabilis*	Brazil	Male	Nazareth and Machado (2009)
	Magnispina neptunus	*Pseudopucrolia sp.*	Brazil	Male	Nazareth and Machado (2010)
	Pseudopucrolia discrepans	*Pseudopucrolia discrepans*	Brazil	Male	Almeida et al. (2020)
Gonyleptidae (Pachylinae)	*Acanthopachylus aculeatus*	*Acanthopachylus aculeatus*	Uruguay	Female	Capocasale and Bruno-Trezza (1964)
	Pachyloidellus goliath	*Pachyloidellus goliath*	Argentina	Female	Photography by C.I. Matoni in Machado and Macías-Ordóñez (2007)
	Pachylus quinamavidensis	*Pachylus quinamavidensis*	Chile	Female	Juberthie and Muñoz-Cuevas (1971)
Gonyleptidae (Progonyleptoidellinae)	*Cadeadoius niger*	*Cadeadoius niger*	Brazil	Male	Stefanini-Jim et al. (1987)
	Deltaspidium orguense	*Geraecormobius orguensis*	Brazil	Male	R. Pinto-da-Rocha, unpub. data in Machado and Raimundo (2001)
	Iguapeia melanocephala	*Iguapeia melanocephala*	Brazil	Male	Machado et al. (2004)
	Iporangaia pustulosa	***Iporangaia pustulosa***	Brazil	Male	Machado et al. (2004) and Requena et al. (2009)
	Progonyleptoidellus striatus	*Progonyleptoidellus striatus*	Brazil	Male	Machado et al. (2004)
Gonyleptidae (Roeweriinae)	*Discocyrtanus oliverioi*	*Discocyrtus oliverioi*	Brazil	Female	Machado et al. (2004)
	Discocyrtanus pertenuis	*Discocyrtus pectinifemur*	Brazil	Female	Matthiesen (1975)
Nomoclastidae	***Quindina albomarginis***	***Zygopachylus albomarginis***	Panama	Male	Rodríguez and Guerrero (1976) and Mora (1990)
Nomoclastidae	***Quindina limbata***	***Quindina limbata***	Costa Rica	Male	Quesada-Hidalgo et al. (2019)
Podoctidae (Ibaloniinae)	*Ibalonoius* sp.*	*Ibalonoius* sp.	Salomon Island	Male	Requena et al. (2013)
	Ibalonoius sp.*	*Ibalonoius* sp.	Philippines	Male	Sharma et al. (2017)
Podoctidae (Podoctinae)	*Borneojapetus* cf. *longipes**	*Japetus* cf. *longipes*	Borneo	Male	Sharma et al. (2017)
	*Leytpodoctis oviger**	*Leytpodoctis oviger*	Philippines	Male	Martens (1993)
Stygnidae (Heterostygninae)	*Eutimesius* sp.	*Eutimesius* sp.	Ecuador	Female	Villareal-Manzanilla and Machado (2011)
	Stenostygnellus aff. *flavolimbatus*	*Stenostygnellus* aff. *flavolimbatus*	Venezuela	Male	Villareal-Manzanilla and Machado (2011)
	Stenostygnellus flavolimbatus	*Stenostygnellus flavolimbatus*	Venezuela	Male	Villareal-Manzanilla and Machado (2011)
Stygnopsidae (Stygnopsinae)	*Serrobunus boneti*	*Hoplobunus boneti*	Mexico	Female	Mitchell (1971)
Triaenonychidae (Sorensenellinae)	*Karamea* spp.	*Karamea* spp.	New Zealand	Male	Forster (1954) and Machado (2007)
	Soerensenella spp.	*Soerensenella* spp.	New Zealand	Male	Forster (1954) and Machado (2007)

All species belong to the suborder Laniatores. Species highlighted in bold indicate cases for which there is experimental or observational evidence on the benefits of parental care.
*There is a discussion in the literature whether the eggs attached to legs of podoctid males are indeed laid by conspecific females (see topic *Forms of Parental Care*). Here, we consider that the most plausible scenario is that males are carrying conspecific eggs and that this behavior is a case of paternal care.

This form of parental care is restricted to the Laniatores, especially those that occur in tropical climates (Machado et al. 2016; Table 2). The protection of the eggs can be performed either by females or males, depending on the species (Figure 9). In species with maternal care, eggs are usually laid synchronously, and females rarely leave the eggs temporarily unattended during embryonic development (e.g., Gnaspini, 1995; Machado and Oliveira 1998, 2002; Willemart and Gnaspini 2004; but see Chelini and Machado 2012; Figure 9A,B). In turn, in species with paternal care, eggs are always

laid asynchronously by different females in a single clutch, and males may abandon their eggs temporarily to forage or take shelter (e.g., Mora 1990; Machado et al. 2004; Figure 9C,D). Another difference between species with maternal and paternal care is that the period of offspring attendance, which occurs when parents remain with the nymphs after hatching (Smiseth et al. 2012), tends to be longer in species with maternal care. In *Acutisoma longipes* (Laniatores: Gonyleptidae), females remain with the nymphs for more than 2 weeks (Machado and Oliveira 1998) whereas in *Iporangaia pustulosa* (Laniatores: Gonyleptidae) males remain with the nymphs for only a few days (Requena et al. 2009). A possible explanation for this difference is that nymphs in species with paternal care can be easily cannibalized by females that visit the oviposition site to lay their own eggs.

Finally, egg carrying, which occurs when parents transport the eggs after laying (Smiseth et al. 2012) is very rare in harvestmen and restricted to the Podoctidae (Laniatores). The first case of this form of paternal care was reported for *Leytpodoctis oviger* (Martens 1993), in which males carry large eggs glued to their hind legs by an adhesive secretion. More recently, Sharma et al. (2017) published a phylogeny of podoctids, with two new reports of species in which males carry eggs on their legs: *Ibalonius* sp. and *Borneojapetus* cf. *longipes*. In the same paper, the authors conducted a paternity test and showed that the eggs glued on the males' legs were not sired by them. Even more surprising, they found a match between the DNA of the eggs and the DNA of spiders.

The findings by Sharma et al. (2017) received strong criticism because some important questions were not addressed by the authors (Machado and Wolf 2018). First, although embryos of different arachnid orders look similar, spider eggs have a granular surface, whereas harvestman eggs have a thick vitelline envelope, with a smooth surface that is usually coated with mucus (Humphreys 1995), as reported for *L. oviger* (Martens 1993). Second, the use of adhesive secretions to attach eggs to the substrate is widespread in harvestmen (Wolff et al. 2016), but not in spiders, in which eggs are usually wrapped in silk (Foelix 2011) and never glued onto surfaces (but see Hawes 2017). Third, spiders lack an ovipositor or any structure that allows females to precisely place their eggs on a thin and short structure, such as the legs of podoctid males. In contrast, harvestman females have an ovipositor that performs precise maneuvers (Martens et al. 1981; Machado and Macías-Ordóñez 2007). Finally, podoctid eggs are consistently attached to males. Given that males and females in Podoctidae are very similar in size and morphology (Kury 2007), it is hard to figure out why spiders would select only males to lay their eggs. Based on the arguments presented above, we argue that the molecular data obtained by Sharma et al. (2017) may have suffered from some contamination. According to our view, the possibility that the eggs attached to the legs of podoctid males belonged to a spider species is very unlikely given what we know about spider morphology and behavior. In conclusion, the presence of paternal care in podoctids remains under debate, and deserves careful consideration, including morphological analyses of the eggs, behavioral observations, and additional paternity tests.

Devoted parents

In the previous topic, we presented examples of species in which parental care is performed either by females or males. Maternal care is relatively common among vertebrates (Balshine 2012) and invertebrates (Trumbo 2012), and harvestmen are not an exception. At least in Laniatores, maternal care has evolved independently at least 10 times (G. Machado unpublished data; see also Table 2). However, paternal care is regarded as one of the rarest forms of parental care among animals. Among arthropods, in particular, recent analyses have shown that paternal care has evolved independently in only 15 lineages, nine of which belonging to the order Opiliones (Requena et al. 2013). This number is impressive as harvestmen represent only 0.6% of all known arthropod diversity but account for 60% of cases of independent evolution of paternal care. The reasons why paternal care has evolved so many times in harvestmen (always in Laniatores) are still unknown, and it is certainly a hot subject for comparative analyses.

Regardless of the sex of the caring individuals, egg attendance, which is the main form of postovipositional care in harvestmen, increases offspring survival. A parent removal experiment has shown that females of the cavernicolous *Phalangodus briareos* (Laniatores: Cranaidae) defend their eggs against predators, especially conspecifics and cave crickets (Figure 9A). When the clutch is left unprotected, almost all eggs are promptly attacked and consumed by predators, indicating that maternal care is crucial for egg survival (García-Hernández and Machado 2018b). Similar results were obtained for other harvestman species with maternal care that live in other habitats, such as *Bourguyia trochanteralis* (Laniatores: Gonyleptidae), which lay their eggs on the vegetation (Machado and Oliveira 2002). Despite the benefits to the offspring, maternal care also imposes costs to females. A long-term field experiment with *Serracutisoma proximum* (Laniatores: Gonyleptidae) has shown that females that were allowed to care for the offspring laid, on average, 15% fewer eggs over the course of their lives when compared with females that were prevented from caring for the offspring. However, because egg attendance greatly improves egg survival, the decision to desert exerts an average reduction of 73% in the females' lifetime fitness (Buzatto et al. 2007).

Parent removal experiments conducted on species with paternal care showed that males also have a crucial role in egg protection. In *Quindina albomarginalis* and *Q. limbata* (Laniatores: Nomoclastidae), egg predation is much lower in nests guarded by males when compared with unguarded nests (Mora 1990; Quesada-Hidalgo et al. 2019; Figure 9D). A similar pattern was found for *Iporangaia pustulosa* (Laniatores: Gonyleptidae), in which males care for eggs laid on the vegetation (Requena et al. 2009). In this species, males stay on the clutches for several weeks and leave the eggs only sporadically to forage or take shelter. This long period of parental care is associated with a reduction in foraging activity that imposes costs to the egg-tending males. During parental care, their body condition deteriorates, and some males in poor-body condition need to desert their clutches to find food (Requena et al. 2012). However, it is important to stress that male mortality during the caring period is lower than in the non-caring period (Requena et al. 2012), as also recorded for *Q. albomarginis* (Requena and Machado 2014). The reasons for this difference in mortality are still not clear and deserve further investigation. One possibility is that harvestmen from tropical regions are mainly attacked by ambush predators, such as spiders (Cokendolpher and Mitov 2007), so that individuals that remain stationary have lower chances of being singled out.

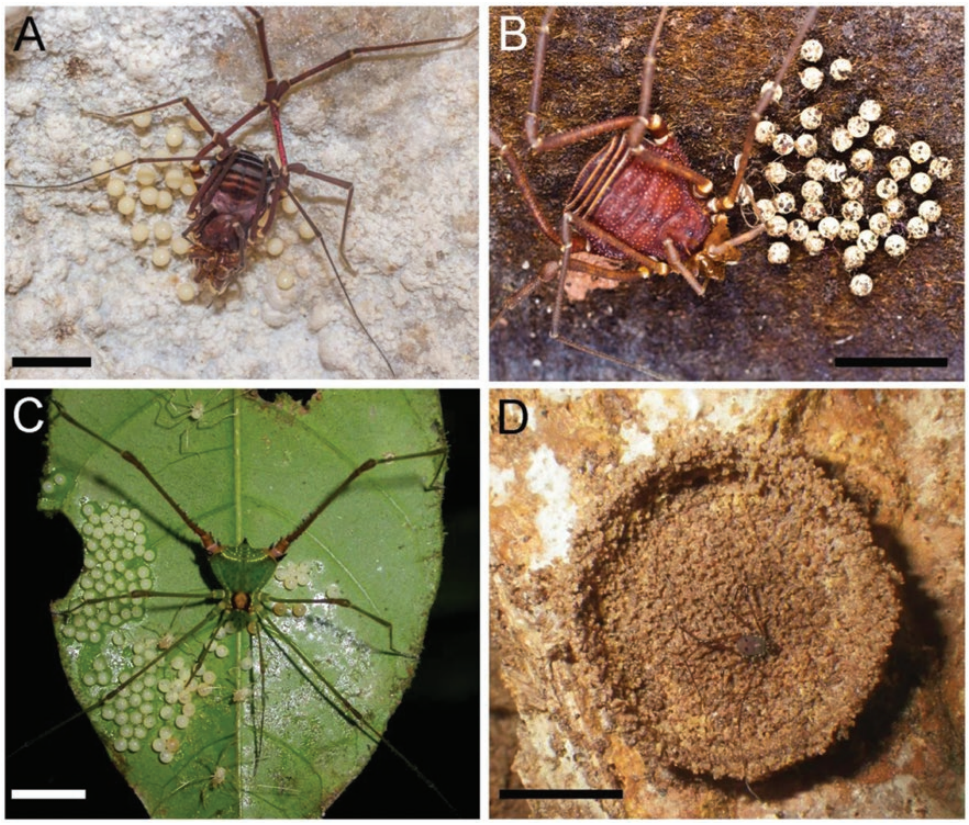

Figure 9 Cases of parental care in harvestmen. (A) Female of *Phalangodus briareos* (Laniatores: Cranaidae) guarding her eggs laid on a cave wall in Colombia (photo by John Uribe). (B) Female of *Discocyrtanus oliverioi* (Laniatores: Gonyleptidae) guarding her eggs under a fallen log in Brazil (photo by John Uribe). Note that the female attaches debris to the surface of the eggs. (C) Male of *Iguapeia melanocephala* (Laniatores: Gonyleptidae) guarding eggs on the undersurface of a leaf in Brazil (photo by Glauco Machado). Recently laid eggs are surrounded by a jelly coat and the clutch is composed of eggs laid by different females at different times. Note the presence of white eggs, which were recently laid, light brown eggs, which are in intermediate stage of embryonic development, and early hatched nymphs. (D) Male of *Quindina limbata* (Laniatores: Nomoclastidae) guarding eggs laid inside a mud nest in Costa Rica. The nests are visited by females that may copulate with the owner male and insert the eggs in the pores of the spongy nest floor (photo by Rosannette Quesada-Hidalgo). Scale bars = ca. 1 cm.

Besides the benefits in terms of reduced mortality, paternal care provides another advantage to the males: females show marked mating preference for egg-tending males. In a double-choice experiment with *Magnispina neptunus* (Laniatores: Gonyleptidae), females rejected males without eggs and preferred to mate and lay eggs in the nests of egg-tending males (Nazareth and Machado 2010). Similar female preferences for egg-tending males were latter reported for *I. pustulosa* under natural field conditions (Requena and Machado 2015), and for other arthropod species, including assassin bugs (Gilbert et al. 2010) and water bugs (Ohba et al. 2016, 2018). In another experiment conducted with *M. neptunus*, unattended nests were visited by both females and males without eggs. While females remained a few minutes or hours inside the nests, showed high propensity to cannibalize eggs, and never repelled conspecifics that entered the nest, males remained inside the nests for several hours or days, showed low propensity to cannibalize eggs, and usually repelled conspecific intruders (Nazareth and Machado 2010). Taken together, female preference for egg-tending males and egg adoption by males without eggs strongly suggest that paternal care is a sexually selected behavior in harvestmen (Requena et al. 2013), as already suggested for other arthropods with exclusive paternal care (Tallamy 2001).

Concluding Remarks

Despite great advances, we still have a lot to learn about the reproductive biology of harvestmen. Most of what has been presented here in the topic *Genital Interactions*, for instance, can be regarded as educated guesses or hypotheses that need to be tested (but see Pérez-González and Werneck 2018). The processes of cryptic female choice and sperm competition, including sperm precedence and benefits of mate guarding, could be explored using paternity analyses. So far, there is only one study of harvestmen that conducted paternity analyses, used to explore the reproductive mode (sexual or sexual) in a facultatively parthenogenetic species (Tyler et al. 2021). The function of nuptial gifts is still not understood and could as easily engender manipulative effects on female fitness as they could be representative of paternal investment (Gwynne 2008). The mechanisms underlying male polymorphism have never been addressed. Among Laniatores, evidence suggests that male dimorphism is a condition-dependent strategy (Buzatto and Machado 2014). In neopilionid Eupnoi, however, male trimorphism seems to be a combination of a condition-dependent strategy and genetic polymorphism (Painting et al. 2015). Finally, although we have accumulated information on the taxonomic distribution of cases of maternal care (Table 2), we still do not fully understand why some species attend their eggs while others hide them and show no

postovipositional care. In the case of species showing paternal care, we know that egg attendance is a sexually selected behavior, but it would be interesting to investigate the factors that determine male attractiveness before they receive their first clutch of eggs, when females have fewer cues about the caring quality of the males.

All questions raised above are only a few examples of the gaps we have in our current knowledge. We anticipate that the coming years will be as exciting as the first 2 decades of the 21st century. Ideally, we will need better representation of taxa because most of what we know is based on a few genera or families, especially in the suborders Eupnoi and Laniatores; representatives of Cyphophthalmi and Dyspnoi are clearly understudied. Moreover, our knowledge is highly concentrated geographically, with the great majority of the studies published with Neotropical species (Figure 1C). This pattern emerged mostly in the beginning of the 21st century, since during the 20th century most studies were published with North American and European species (Machado et al. 2007). Nowadays, there are few researchers in temperate regions fully devoted to studying harvestmen biology, and to our knowledge, there are no researchers in Africa and Asia working on reproduction in harvestmen. We hope the information synthesized in this review will stimulate more people worldwide to embrace harvestmen as their study system and to improve our effort to unravel the mysteries of their reproductive biology.

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Conflict of Interest

We declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

References

Alcock J, 1994. Post-insemination associations between males and females in insects: the mate-guarding hypothesis. *Ann Rev Entomol* **39**:1–21.

Aisenberg A, Barrantes G, Eberhard WG, 2015. Post-copulatory sexual selection in two tropical orb-weaving *Leucauge* spiders. In: Peretti AV, Aisenberg A, editors. *Cryptic Female Choice in Arthropods: Patterns, Mechanisms and Prospects*. Berlin: Springer.

Almeida TRB, Santos M, De Souza AM, Moura GJB, Lira AFA, 2020. Cuidado parental do opilião *Pseudopucrolia discrepans* (Roewer, 1943). In: "VI Congresso Latino-Americano de Aracnologia". Buenos Aires, Argentina.

Ázara LN, DaSilva MB, Ferreira RL, 2013. Description of *Mitogoniella mucuri* sp. nov. (Opiliones: Gonyleptidae) and considerations on polymorphic traits in the genus and Gonyleptidae. *Zootaxa* **3736**:69–81.

Balshine S, 2012. Patterns of parental care in vertebrates. In: Royle NJ, Smiseth PT, Kölliker M, editors. *The Evolution of Parental Care*. Oxford: Oxford University Press.

Belozerov VN, 2012. Dormant stages and their participation in adjustment and regulation of life cycles of harvestmen (Arachnida, Opiliones). *Entomol Rev* **92**:688–713.

Bernardo J, 1996. Maternal effects in animal ecology. *Am Zool* **36**:83–105.

Bernays EA, Chapman RF, 1994. *Host-plant Selection by Phytophagous Insects*. New York: Chapman and Hall.

Briggs T, 1971. Relict harvestmen from the Pacific northwest. *Pan-Pacific Entomol* **47**:165–178.

Brown T, Tsurusaki N, Burns M, 2021. Genomic determination of reproductive mode in facultatively parthenogenetic Opiliones. *J Hered* **112**:34–44.

Burke NW, Bonduriansky R, 2019. The paradox of sex: The roles of sexual conflict and mate scarcity in transitions to facultative and obligate asexuality. *J Evol Biol* **32**:1230–1241.

Burke NW, Bonduriansky R, 2022. Sexually but not parthenogenetically produced females benefit from mating in a stick insect. *Func Ecol*. 36:2001–2014. doi:10.1111/1365-2435.14095.

Burns M, Shultz JW, 2016. Mechanical properties of male genitalia in *Leiobunum* harvestmen (Arachnida, Opiliones, Sclerosomatidae). *J Arachnol* **44**:199–209.

Burns M, Tsurusaki N, 2016. Male reproductive morphology across latitudinal clines and under long-term female sex ratio bias. *Integ Comp Biol* **56**:715–727.

Burns M, Hedin M, Shultz JW, 2015. Biomechanical diversity of mating structures among harvestmen is consistent with a spectrum of precopulatory strategies. *PLoS ONE* **10**:e0137181.

Burns M, Hedin M, Tsurusaki N, 2018. Population genomics and geographical parthenogenesis in Japanese harvestmen (Opiliones, Sclerosomatidae, *Leiobunum*). *Ecol Evol* **8**:36–52.

Burns M, Hedin M, Shultz JW, 2013. Comparative analyses of reproductive structures in harvestmen (Opiliones) reveal multiple transitions from courtship to precopulatory antagonism. *PLoS ONE* **8**:e66767.

Buzatto BA, Machado G, 2008. Resource defense polygyny shifts to female defense polygyny over the course of the reproductive season of a Neotropical harvestman. *Behav Ecol Sociobiol* **63**:85–94.

Buzatto BA, Machado G, 2014. Male dimorphism and alternative reproductive tactics in harvestmen (Arachnida: Opiliones). *Behav Proc* **109**:2–13.

Buzatto BA, Requena GS, Martins EG, Machado G, 2007. Effects of maternal care on the lifetime reproductive success of females in a Neotropical harvestman. *J Anim Ecol* **76**:937–945.

Buzatto BA, Requena GS, Lourenço RS, Munguía-Steyer R, Machado G, 2011. Conditional male dimorphism and alternative reproductive tactics in a Neotropical arachnid (Opiliones). *Evol Ecol* **25**:331–349.

Buzatto BA, Tomkins JL, Simmons LW, Machado G, 2014. Correlated evolution of sexual dimorphism and male dimorphism in a clade of neotropical harvestmen. *Evolution* **68**:1671–1686.

Buzatto BA, Macías-Ordóñez R, Machado G, 2013. Macroecology of harvestman mating systems. In: Macedo RH, Machado G, editors. *Sexual Selection: Perspectives and Models from the Neotropics*. Amsterdam: Elsevier.

Caetano DS, Machado G, 2013. The ecological tale of Gonyleptidae (Arachnida, Opiliones) evolution: phylogeny of a Neotropical lineage of armoured harvestmen using ecological, behavioural and chemical characters. *Cladistics* **29**:589–609.

Calbacho-Rosa L, Galicia-Mendoza I, Dutto MS, Córdoba-Aguilar A, Peretti AV, 2013. Copulatory behavior in a pholcid spider: Males use specialized genitalic movements for sperm removal and copulatory courtship. *Naturwissenschaften* **100**:407–416.

Calbacho-Rosa L, Peretti AV, 2015. Copulatory and post-copulatory sexual selection in haplogyne spiders, with emphasis on Pholcidae and Oonopidae. In: Peretti AV, Aisenberg A, editors. *Cryptic Female Choice in Arthropods: Patterns, Mechanisms and Prospects*. Berlin: Springer.

Canals J, 1936. Observaciones biológicas en arácnidos del orden Opiliones. *Rev Chilena Hist Nat* **40**:61–63.

Capocasale RM, Bruno-Trezza L, 1964. Biología de *Acanthopachylus aculeatus* (Kirby, 1819) (Opiliones: Pachylinae). *Rev Soc Uruguaya Entomol* **6**:19–32.

Chelini MC, Machado G, 2012. Costs and benefits of temporary brood desertion in a Neotropical harvestman (Arachnida: Opiliones). *Behav Ecol Sociobiol* **66**:1619–1627.

Chelini MC, Machado G, 2014. Multiple lines of egg defense in a Neotropical arachnid with temporary brood desertion. *Ethology* **120**:1147–1154.

Clawson RL, 1988. Morphology of defense glands of the opilionids (daddy longlegs) *Leiobunum vittatum* and *Leiobunum flavum* (Arachnida: Opiliones: Palpatores: Phalangiidae). *J Morphol* **196**:363–381.

Cokendolpher JC, Mitov PG, 2007. Natural enemies. In: Pinto-da-Rocha R, Machado G, Giribet G, editors. *Harvestmen: The Biology of Opiliones*. Cambridge: Harvard University Press.

Colmenares AL, Tourinho AL, 2014. Two new species of *Phareicranaus* Roewer 1913 (Opiliones: Laniatores: Cranaidae), with notes on gregarious behavior and maternal care in *Phareicranaus manauara*. *Zootaxa* **3768**:59–72.

Damron BN, Sagastume-Espinoza KO, Longhorn SJ, 2021. Paternal care in the Neotropical harvestman *Cynorta bromeliacia* (Opiliones: Cosmetidae). *J Arachnol* **49**:151–155.

Dougherty LR, Skirrow MJA, Jennions MD, Simmons LW, 2022. Male alternative reproductive tactics and sperm competition: a meta-analysis. *Biol Rev* **97**:1365–1388.

Eberhard WG, 2015. Cryptic female choice and other types of post-copulatory sexual selection. In: Peretti AV, Aisenberg A, editors. *Cryptic Female Choice in Arthropods: Patterns, Mechanisms and Prospects*. Berlin: Springer.

Eberhard WG, Rodríguez RL, Huber BA, Speck B, Miller H et al., 2018. Sexual selection and static allometry: The importance of function. *Quart Rev Biol* **93**:207–250.

Edgar AL, 1971. Studies on the biology and ecology of Michigan Phalangida (Opiliones). *Misc Pub Mus Zool, Univ Mich* **144**:1–64.

Elgar MA, 1992. Sexual cannibalism in spiders and other invertebrates. In: Elgar MA, Crespi BJ, editors. *Cannibalism: Ecology and Evolution among Diverse Taxa*. Oxford: Oxford University Press.

Emlen ST, Oring LW, 1977. Ecology, sexual selection, and evolution of mating systems. *Science* **197**:215–223.

Fernández R, Sharma PP, Tourinho AL, Giribet G, 2017. The Opiliones tree of life: Shedding light on harvestmen relationships through transcriptomics. *Proc R Soc B* **284**:20162340.

Foelix RF, 2011. *Biology of Spiders*. Oxford: Oxford University Press.

Forster RR, 1954. The New Zealand harvestmen (sub-order Laniatores). *Canterbury Mus Bull* **2**:1–329.

Fowler-Finn KD, Triana E, Miller OG, 2014. Mating in the harvestman *Leiobunum vittatum* (Arachnida: Opiliones): From premating struggles to solicitous tactile engagement. *Behaviour* **151**:1663–1686.

Fowler-Finn KD, Boyer SL, Ikagawa R, Jeffries T, Kahn PC, Larsen EM, Lee D, Smeester M, 2018. Variation in mating dynamics across five species of leiobunine harvestmen (Arachnida: Opiliones). *Biology* **7**:36.

Fowler-Finn KD, Boyer SL, Ikagawa R, Jeffries T, Kahn PC, Larsen EM, Lee D, Smeester M. 2019. Qualitative and quantitative comparisons of mating behaviour across multiple populations and six species of leiobunine harvestmen (Arachnida: Opiliones). *Behaviour* **156**:363–390

Gadgil M, 1972. Male dimorphism as a consequence of sexual selection. *Am Nat* **106**:574–580.

García-Hernández S, Machado G, 2018a. Effectiveness of maternal egg attendance in an exclusively cave-dwelling harvestman (Arachnida: Opiliones). *J Zool* **302**:228–235.

García-Hernández S, Machado G, 2018b. Convergent fighting behavior in two species of Neotropical harvestmen (Opiliones): Insights on the evolution of maternal care and resource defense polygyny. *J Arachnol* **46**:165–169.

Gilbert JDJ, Thomas LK, Manica A, 2010. Quantifying the benefits and costs of parental care in assassin bugs. *Ecol Entomol* **35**:639–651.

Gnaspini P, 1995. Reproduction and postembryonic development of *Goniosoma spelaeum*, a cavernicolous harvestman from southeastern Brazil (Arachnida: Opiliones: Gonyleptidae). *Invert Reprod Develop* **28**:137–151.

Gnaspini P, 2007. Development. In: Pinto-da-Rocha R, Machado G, Giribet G, editors. *Harvestmen: The Biology of Opiliones*. Cambridge: Harvard University Press.

Gnaspini P, Hara MR, 2007. Defense mechanisms. In: Pinto-da-Rocha R, Machado G, Giribet G, editors. *Harvestmen: The Biology of Opiliones*. Cambridge: Harvard University Press.

González-Sponga MA, 1992. Arácnidos de Venezuela. Nueva especie del género *Acropsopilio*de la Cordillera de la Costa (Caddidae). *Bol Acad Cienc Fís, Matem Nat* **52**:43–51.

Goodnight CJ, Goodnight ML, 1976. Observations on the systematics, development and habits of *Erginulus clavotibialis* (Opiliones: Cosmetidae). *Trans Am Microscop Soc* **95**:654–664.

Gross MR, 1996. Alternative reproductive strategies and tactics: Diversity within sexes. *Trends Ecol Evol* **11**:92–98.

Gruber J, 1974. Bemerkungen zur Morphologie und systematischen Stellung von *Caddo, Acropsopilio*und verwandter formen (Opiliones, Arachnida). *Annal Naturhistor Mus Wien* **78**:237–259.

Gwynne DT, 2008. Sexual conflict over nuptial gifts in insects. *Annu Rev Entomol* **53**:83–101.

Hara MR, Gnaspini P, Machado G, 2003. Male guarding behavior in the Neotropical harvestman *Ampheres leucopheus* (Mello-Leitão 1922) (Opiliones, Laniatores, Gonyleptidae). *J Arachnol* **31**:441–444.

Haubruge E, Arnaud L, Mignon J, Gage MJG, 1999. Fertilization by proxy: Rival sperm removal and translocation in a beetle. *Proc R Soc B* **266**:1183–1187.

Hawes TC, 2017. A jumping spider that lays eggs like an insect. *Invert Reprod Dev* **61**:265–273.

Herberstein ME, Painting CJ, Holwell GI, 2017. Scramble competition polygyny in terrestrial arthropods. *Adv Stud Behav* **49**:237–295.

Hotzy C, Polak M, Rönn JL, Arnqvist G, 2012. Phenotypic engineering unveils the function of genital morphology. *Cur Biol* **22**:2258–2261.

Humphreys WF, 1995. Chorion surface features of chelicerate eggs. *Rec West Aust Mus* **52S**:171–181.

Immel V, 1954. Zur Biologie und Physiologie von *Nemastoma quadripunctatum* (Opiliones, Dyspnoi). *Zool Jahre* **83**:129–184.

Jaron KS, Bast J, Nowell RW, Ranallo-Benavidez TR, Robinson-Rechavi M et al., 2021. Genomic features of parthenogenetic animals. *J Hered* **112**:19–33.

Juberthie C, Muñoz-Cuevas A, 1971. Sur la ponte de *Pachylus quinamavidensis* (Opilion, Gonyleptidae). *Bull Soc Hist Nat Toulouse* **107**:468–474.

Kahn PC, Cao DD, Burns M, Boyer SL, 2018. Nuptial gift chemistry reveals convergent evolution correlated with antagonism in mating systems of harvestmen (Arachnida, Opiliones). *Ecol Evol* **8**:7103–7110.

Kamimura Y, 2005. Last-male paternity of *Euborellia plebeja*, an earwig with elongated genitalia and sperm-removal behavior. *J Ethol* **23**:35–41.

Karachiwalla Z, de Carvalho T, Burns M, 2020. Spermathecal variation in temperate Opiliones. *Integ. Compar Biolicaa* **120**:1–10.

Karaman IM, 2005. Evidence of spermatophores in Cyphophthalmi (Arachnida, Opiliones). *Rev Suisse Zool* **112**:3–11.

Kokko H, Klug H, Jennions MD, 2014. Mating systems. In: Shuker DM, Simmons LW, editors. *The Evolution of Mating Systems in Insects*. Oxford: Oxford University Press.

Kury AB, 2007. Podoctidae Roewer, 1912. In: Pinto-da-Rocha R, Machado G, Giribet G, editors. *Harvestmen: The Biology of Opiliones*. Cambridge: Harvard University Press.

Kury AB, Mendes AC, Cardoso L, Kury MS, Granado AA et al., 2021. WCO-Lite version 1.1: an online nomenclatural catalogue of harvestmen of the world (Arachnida, Opiliones) curated in TaxonWorks. *Zootaxa* **4908**:447–450.

Kustra MC, Alonzo SH, 2020. Sperm and alternative reproductive tactics: a review of existing theory and empirical data. *Philos Trans R Soc B* **375**:20200075.

Machado G, 2002. Maternal care, defensive behavior, and sociality in Neotropical *Goniosoma* harvestmen (Arachnida, Opiliones). *Insect Soc* **49**:1–6.

Machado G, 2007. Maternal or paternal egg guarding? Revisiting parental care in triaenonychid harvestmen (Opiliones). *J Arachnol* **35**:202–204.

Machado G, Warfel J, 2006. First case of maternal care in the family Cranaidae (Opiliones, Laniatores). *J Arachnol* **34**:269–272.

Machado G, Wolf JO, 2018. The assassination of a hypothesis by non-critical interpretation of molecular data: A comment on Sharma *et al*. (2017). *Mol Phylogenet Evol* **129**:346–348.

Machado G, Oliveira PS, 1998. Reproductive biology of the neotropical harvestman *Goniosoma longipes* (Arachnida, Opiliones: Gonyleptidae): Mating and oviposition behaviour, brood mortality and parental care. *J Zool* **246**:359–367.

Machado G, Oliveira PS, 2002. Maternal care in the Neotropical harvestman *Bourguyia albiornata* (Arachnida: Opiliones): oviposition site selection and egg protection. *Behaviour* **139**:1509–1524.

Machado G, Macías-Ordóñez R, 2007. Reproduction. In: Pinto-da-Rocha R, Machado G, Giribet G, editors. *Harvestmen: The Biology of Opiliones*. Cambridge: Harvard University Press.

Machado G, Pinto-da-Rocha R, Giribet G, 2007. What are harvestmen? In: Pinto-da-Rocha R, Machado G, Giribet G, editors. *Harvestmen: The Biology of Opiliones*. Cambridge: Harvard University Press.

Machado G, Raimundo RLG, 2001. Parental investment and the evolution of subsocial behaviour in harvestmen (Arachnida: Opiliones). *Ethol Ecol Evol* **13**:133–150.

Machado G, Giaretta AA, Pinto-da-Rocha R, 2001. Notes on the taxonomy and biology of the neotropical harvestman *Goniosoma catarina* sp.n. (Opiliones: Gonyleptidae). *Rev Ibér Aracnol* **4**:17–22.

Machado G, Buzatto BA, García-Hernández S, Macías-Ordóñez R, 2016. Macroecology of sexual selection: A predictive conceptual framework for large-scale variation in reproductive traits. *Am Nat* **188**:S8–S27.

Machado G, Requena GS, Buzatto BA, Osses F, Rossetto LM, 2004. Five new cases of paternal care in harvestmen (Arachnida: Opiliones): Implications for the evolution of male guarding in the neotropical family Gonyleptidae. *Sociobiology* **44**:577–598.

Machado G, Requena GS, Toscano-Gadea C, Stanley E, Macías-Ordóñez R, 2015. Male and female mate choice in harvestmen: General patterns and inferences on the underlying processes. In: Peretti AV, Aisenberg A, editors. *Cryptic Female Choice in Arthropods: Patterns, Mechanisms and Prospects*. Berlin: Springer.

Machado SF, Ferreira RL, Martins RP, 2003. Aspects of the population ecology of *Goniosoma* sp. (Arachnida, Opiliones, Gonyleptidae) in limestone caves in southeastern Brazil. *Trop Zool* **16**:13–31.

Macías-Ordóñez R, 1997. *The Mating System of Leiobunum vittatum Say 1821 (Arachnida: Opiliones: Palpatores): Resource Defense Polygyny in the Striped Harvestman*. PhD thesis, Lehigh University.

Macías-Ordóñez R, 2000. Touchy harvestmen. *Nat Hist* **109**:58–67.

Macías-Ordóñez R, Machado G, Pérez-González A, Shultz JW, 2010. Genitalic evolution in Opiliones. In: Leonard J, Córdoba-Aguilar A, editors. *The Evolution of Primary Sexual Characters in Animals*. New York: Oxford University Press.

Martens J, 1969. Die Sekretdarbietung während des Paarungsverhaltens von *Ischyropsalis* C. L. Koch (Opiliones). *Z Tierpsychol* **26**:513–523.

Martens J, 1978. *Spinnentiere, Arachnida: Weberknechte, Opiliones*. *Die Tierwelt Deutschlands*. Vol. **64**. Jena: G. Fischer Verlag.

Martens J, 1993. Further cases of paternal care in Opiliones (Arachnida). *Trop Zool* **6**:97–107.

Martens J, Hoheisel U, Götze M, 1981. Vergleichende Anatomie der Legeröhren der Opiliones als Beitrag zur Phylogenie der Ordnung (Arachnida). *Zool Jb Anat* **105**:13–76.

Matthiesen FA, 1975. Sobre a postura de *Discocyrtus pectinifemur*-Mello-Leitão, 1937 (Opiliones, Gonyleptidae). *Ciência Cultura* **35**:1339–1341.

Maury EA, Pinto-da-Rocha R, Morrone JJ, 1996. Distribution of *Acropsopilio chilensis* Silvestri, 1904 in southern South America (Opiliones, Palpatores, Caddidae). *Biogeographica* **72**:127–132.

McCartney J, Shear W, Stringer IAN, 2007. New records of *Acropsopilio neozealandiae* (Forster), and remarks on the sexual status of the species (Arachnida: Opiliones: Caddidae). *N Z J Zool* **34**:117–123.

Meijer J, 1972. Some data on the phenology and the activity patterns of *Nemastoma lugubre* (Müller) and *Mitostoma chrysomelas* (Herman) (Nemastomatidae: Opilionida: Arachnida). *Netherl J Zool* **22**:105–118.

Mitchell RW, 1971. Egg and young guarding by a cave-dwelling harvestman *Hoplobunus boneti* (Arachnida). *Southweast Nat* **15**:392–395.

Montgomerie RD, Weatherhead PJ, 1988. Risks and rewards of nest defence by parent birds. *Q Rev Biol* **63**:167–187.

Mora G, 1990. Parental care in a Neotropical harvestman *Zygopachylus albomarginis* (Arachnida: Gonyleptidae). *Anim Behav* **39**:582–593.

Morrow EH, 2004. How the sperm lost its tail: the evolution of a flagellate sperm. *Biol Rev* **79**:795–814.

Morse DH, 1985. Nests and nest-site selection of the crab spider *Misumena vatia* (Aranae, Thomisidae) on milkweed. *J Arachnol* **13**:383–390.

Munguía-Steyer R, Buzatto BA, Machado G, 2012. Male dimorphism of a neotropical arachnid: Harem size, sneaker opportunities, and gonadal investment. *Behav Ecol* **23**:827–835.

Muniz DG, Buzatto BA, Guimarães PR Jr, Machado G, 2015. A sexual network approach to sperm competition in a species with alternative mating tactics. *Behav Ecol* **26**:121–129.

Muster C, Böttcher B, Komposch C, Knoflach B, 2005. Bisexuals surrounded by all-female clones: New records of *Megabunus lesserti* (Opiliones: Phalangiidae) in the northeastern Alps. *Arachnol Mitteil* **30**:20–24.

Nazareth TM, Machado G, 2009. Reproductive behavior of *Chavesincola inexpectabilis* (Opiliones, Gonyleptidae) with description of a new and independently evolved case of paternal care in harvestmen. *J Arachnol* **37**:127–134.

Nazareth TM, Machado G, 2010. Mating system and exclusive postzygotic paternal care in a Neotropical harvestman (Arachnida: Opiliones). *Anim Behav* **79**:547–554.

Ohba SY, Okuda N, Kudo SI, 2016. Sexual selection of male parental care in giant water bugs. *R Soc Open Sci* **3**:150720.

Ohba SY, Matsuo S, Huynh TTT, Kudo SI, 2018. Female mate preference for egg-caring males in the giant water bug *Diplonychus rusticus* (Heteroptera: Belostomatidae). *Ethol Ecol Evol* **30**:477–484.

Oliveira RF, Taborsky M, Brockmann HJ, 2008. *Alternative Reproductive Tactics: An Integrative Approach*. Cambridge: Cambridge University Press.

Osses F, Martins EG, Machado G, 2008. Oviposition site selection by the bromeliad-dweller harvestman *Bourguyia hamata* (Arachnida: Opiliones). *J Ethol* **26**:233–241.

Pabst W, 1953. Zur Biologie der mitteleuropäischen Troguliden. *Zool Jb Abt Syst Ökol u Geog Tiere* **82**:1–156.

Painting CJ, Probert AF, Townsend DJ, Holwell GI, 2015. Multiple exaggerated weapon morphs: a novel form of male polymorphism in harvestmen. *Sci Rep* **5**:16368.

Palaoro AV, García-Hernández S, Buzatto BA, Machado G, 2022. Function predicts the allometry of contest-related traits, but not sexual or male dimorphism in the Amazonian tusked harvestman. *Evol Ecol* **36**: 605–630.

Parisot C, 1962. Étude de quelques opilions de Lorraine. *Vie et Millieu* **13**:179–197.

Parker GA, 1970. Sperm competition and its evolutionary consequences in the insects. *Biol Rev Camb Philos Soc* **45**:525–567.

Parker GA, 1990. Sperm competition games: sneaks and extra-pair copulations. *Proc R Soc B* **242**:127–133.

Pérez-González A, Werneck RM, 2018. A fresh look over the genital morphology of *Triaenonychoides* (Opiliones: Laniatores: Triaenonychidae) unravelling for the first time the functional morphology of male genitalia. *Zool Anz* **272**:81–92.

Phillipson J, 1959. The seasonal occurrence, life histories and fecundity of harvest-spiders (Phalangida, Arachnida) in neighborhood of Durham City. *Entomol Monthly Mag* **95**:134–138.

Pinto-da-Rocha R, 1993. Invertebrados cavernícolas da porção meridional da Província Espeleológica do Vale do Ribeira, Sul do Brasil. *Revta Bras Zool* **10**:229–255.

Pinto-da-Rocha R, Machado G, Giribet G, 2007. *Harvestmen: The Biology of Opiliones*. Cambridge: Harvard University Press.

Pizzari T, Parker GA, 2009. Sperm competition and sperm phenotype. In: Birkhead TR, Hosken DJ, Pitnick S, editors. *Sperm Biology: An evolutionary Perspective*. Burlington: Elsevier.

Powell EC, Painting CJ, Hickey AJ, Holwell GI, 2020. Defining an intrasexual male weapon polymorphism in a New Zealand harvestman (Opiliones: Neopilionidae) using traditional and geometric morphometrics. *Biol J Linn Soc* **130**:395–409.

Powell EC, Willmott NJ, Selleck CJ, Painting CJ, Hickey AJ et al., 2021. No risk to scrambling? Mating tactic does not affect the frequency of leg autotomy in a New Zealand harvestman. *Anim Behav* **177**:99–106.

Proud DN, Víquez C, Townsend VR Jr., 2011. Paternal care in a Neotropical harvestman (Opiliones: Cosmetidae) from Costa Rica. *J Arachnol* **39**:497–499.

Quesada-Hidalgo R, Solano-Brenes D, Requena GS, Machado G, 2019. The good fathers: Efficiency of exclusive paternal care and the role of foster parents as egg protectors in a Neotropical arachnid. *Anim Behav* **150**:147–155.

Ramires EN, Giaretta AA, 1994. Maternal care in a neotropical harvestman *Acutisoma proximum* (Opiliones, Gonyleptidae). *J Arachnol* **22**:179–180.

Refsnider JM, Janzen FJ, 2010. Putting eggs in one basket: Ecological and evolutionary hypotheses for variation in oviposition-site choice. *Ann Rev Ecol Evol Syst* **41**:39–57.

Requena GS, Machado G, 2014. Lack of costs associated with nest-related behaviors in an arachnid with exclusive paternal care. *Oikos* **124**:372–380.

Requena GS, Machado G, 2015. Effects of egg attendance on male mating success in a harvestman with exclusive paternal care. *Behav Ecol* **26**:926–935.

Requena GS, Buzatto BA, Martins EG, Machado G, 2012. Paternal care decreases foraging activity and body condition, but does not impose survival costs to caring males in a Neotropical arachnid. *PLoS ONE* **7**:e46701.

Requena GS, Buzatto BA, Munguía-Steyer R, Machado G, 2009. Efficiency of uniparental male and female care against egg predators in two closely related syntopic harvestmen. *Anim Behav* **78**:1169–1176.

Requena GS, Munguía-Steyer R, Machado G, 2013. Paternal care and sexual selection in arthropods. In: Macedo RH, Machado G, editors. *Sexual Selection: Perspectives and Models from the Neotropics*. Amsterdam: Elsevier.

Robinson MH, 1982. Courtship and mating behavior in spiders. *Ann Rev Entomol* **27**:1–20.

Rodríguez CA, Guerrero S, 1976. La historia natural y el comportamiento de *Zygopachylus albomarginis* (Chamberlin) (Arachnida: Opiliones: Gonyleptidae). *Biotropica* **8**:242–247.

Rojas A, Solano-Brenes D, Muniz DG, Machado G, 2019. Gone with the rain: Negative effects of rainfall on male reproductive success in a nest-building arachnid. *Behav Ecol* **30**:1145–1156.

Rojas A, Solano-Brenes D, Muniz DG, Machado G, 2021. Nest-site selection in a neotropical arachnid with exclusive male care: Proximate cues and adaptive meaning. *Ethology* **127**:334–341.

Romero GQ, Vasconcellos-Neto J, 2005. The effects of plant structure on the spatial and microspatial distribution of a bromeliad-living jumping spider (Salticidae). *J Anim Ecol* **74**:12–21.

Sasson DA, Johnson TD, Scott ER, Fowler-Finn KD, 2020. Short-term water deprivation has widespread effects on mating behaviour in a harvestman. *Anim Behav* **165**:97–106.

Schwendinger PJ, Giribet G, 2005. The systematics of the south-east Asian genus *Fangensis* Rambla, 1994 (Opiliones: Cyphophthalmi: Stylocellidae). *Invertebr Syst* **19**: 297–323.

Sharma PP, Santiago MA, Savana RK, Lippsa Perry M, Buenavente AC et al., 2017. A multilocus phylogeny of Podoctidae (Arachnida, Opiliones, Laniatores) and parametric shape analysis reveal the disutility of subfamilial nomenclature in armored harvestman systematics. *Mol Phylog Evol* **106**:164–173.

Shear WA, 1974. The opilionid family Caddidae in North America, with notes on species from other regions (Opiliones, Palpatores, Caddoidea). *J Arachnol* **2**:65–88.

Shear WA, 2004. Description of the female of *Acropsopilio chomulae* (Goodnight and Goodnight 1948) from Chiapas, Mexico (Opiliones, Caddidae, Acropsopilioninae). *J Arachnol* **32**:432–435.

Shine R, Olsson MM, Mason RT, 2000. Chastity belts in gartersnakes: The functional significance of mating plugs. *Biol J Linn Soc* **70**:377–390.

Shultz JW, Regier JC, 2009. *Caddo agilis* and *Caddo pepperella* (Opiliones: Caddidae) diverged phylogenetically before acquiring their disjunct, sympatric distributions in Japan and North American. *J Arachnol* **37**:238–240.

Simmons LW, 2001. *Sperm Competition and Its Evolutionary Consequences in the Insects*. Princeton: Princeton University Press.

Simmons LW, 2014. Sexual selection and genital evolution. *Austral Entomol* **53**:1–17.

Smiseth PT, Kölliker M, Royle NJ, 2012. What is parental care? In: Royle NJ, Smiseth PT, Kölliker M, editors. *The Evolution of Parental Care*. Oxford: Oxford University Press.

Solano-Brenes D, García-Hernández S, Machado G, 2018. All the better to bite you with! Striking intrasexual differences in cheliceral size define two male morphs in an Amazonian arachnid. *Biol J Linn Soc* **125**:521–534.

Stanley S, Machado G, Aisenberg A. Sexual dialogue in *Pachyloides thorellii* (Opiliones: Gonyleptidae): A Neotropical harvestman with much to say. *J Arachnol*. In press.

Stefanini-Jim RL, Soares HEM, Jim J, 1987. Notas sobre a biologia de *Cadeadoius niger* (Mello-Leitão, 1935) (Opiliones, Gonyleptidae, Progonyleptoidellinae), pp. 24. In: *Anais do XX Encontro Brasileiro de Etologia*. Botucatu, São Paulo, Brazil.

Suzuki S, 1972. On the discontinuous distribution in some Opiliones. *Acta Arachnol* **24**: 1–8 (In Japanese with English abstract).

Suzuki S, 1976. The harvestmen of family Caddidae in Japan (Opiliones, Palpatores, Caddoidea). *J Sci Hiroshima Univ, Ser B, Div 1 (Zoology)* **26**:261–273.

Suzuki S, 1978. Three harvestmen (Arachnida, Opiliones) from the Bonin Islands. *Annot Zool Japon* **51**:179–185.

Suzuki S, Tomishima K, Yano S, Tsurusaki N, 1977. Discontinuous distribution in relict harvestmen (Opiliones, Arachnida). *Acta Arachnol* **27**: 121–138 (In Japanese with English abstract).

Suzuki S, Tsurusaki N, 1983. Opilionid fauna of Hokkaido and its adjacent areas. *J Sci Hiroshima Univ, Ser B, Div 1 (Zool)* **23**:195–243.

Tallamy DW, 2001. Evolution of exclusive paternal care in arthropods. *Annu Rev Entomol* **46**:139–165.

Thomas RH, Zeh DW, 1984. Sperm transfer and utilization strategies in arachnids: ecological and morphological constraints. In: Smith RL editor. *Sperm Competition and Evolution of Animal Mating Systems*. Orlando: Academic Press.

Tischler W, 1967. Zur Biologie und Ökologie des Opilioniden *Mitopus morio* F. *Biol Zentralblatt* **86**:473–484.

Townsend VR Jr, Bertram MS, Milne MA, 2015. Variation in ovipositor morphology among laniatorean harvestmen (Arachnida: Opiliones). *Zoomorphology* **134**:487–497.

Townsend VR Jr, Pérez-González A, Proud DN, 2019. Putative mating plugs of harvestmen (Opiliones, Laniatores). *Zool Anzeig* **278**:101–109.

Trumbo ST, 2012. Patterns of parental care in invertebrates. In: Royle NJ, Smiseth PT, Kölliker M, editors. *The Evolution of Parental Care*. Oxford: Oxford University Press.

Tsurusaki N, 1986. Parthenogenesis and geographic variation of sex ratio in two species of *Leiobunum* (Arachnida, Opiliones). *Zool Sci* **3**:517–532.

Tyler AB, Tsurusaki N, Burns M, 2021. Genomic determination of reproductive mode in facultatively parthenogenetic Opiliones. *J Hered* **2021**:1–11.

Uhl G, Nessler S, Schneider J, 2010. Securing paternity in spiders? A review on occurrence and effects of mating plugs and male genital mutilation. *Genetica* **138**:75–104.

van der Hammen L, 1985. Comparative studies in Chelicerata. III. Opilionida. *Zool Verhand* **220**:1–60.

Villareal-Manzanilla O, Machado G, 2011. First record of paternal care in the family Stygnidae (Opiliones: Laniatores). *J Arachnol* **39**:500–502.

von Helversen D, von Helversen O, 1991. Pre-mating sperm removal in the bushcricket *Metaplastes* Ramme 1931 (Orthoptera, Tettigonoidea, Phaneropteridae). *Behav Ecol Sociobiol* **28**:391–396.

Waage JK, 1979. Dual function of the damselfly penis: Sperm removal and transfer. *Science* **203**:916–918.

Wachter GA, Papadopoulou A, Muster C, Arthofer W, Knowles LL et al., 2016. Glacial refugia, recolonization patterns and diversification forces in Alpine-endemic *Megabunus harvestmen*. *Mol Ecol* **25**:2904–2919.

Werneck RM, Caetano DS, Machado G, 2012. Maternal care in the Neotropical harvestman *Liogonyleptoides tetracanthus* (Opiliones: Gonyleptidae). *J Arachnol* **40**:135–137.

Wijnhoven H, 2011. Notes on the biology of the unidentified invasive harvestman *Leiobunum* sp. (Arachnida: Opiliones). *Arachnol Mitt* **41**:17–30.

Willemart RH, Gnaspini P, 2004. Breeding biology of the cavernicolous harvestman *Goniosoma albiscriptum* (Arachnida, Opiliones, Laniatores): Sites of oviposition, egg batches characteristics and subsocial behaviour. *Invert Reprod Dev* **45**:15–28.

Willemart RH, Farine JP, Peretti AV, Gnaspini P, 2006. Behavioral roles of the sexually dimorphic structures in the male harvestman *Phalangium opilio* (Opiliones, Phalangiidae). *Can J Zool* **84**:1763–1774.

Wolff JO, García-Hernández S, Gorb SN, 2016. Adhesive secretions in harvestmen (Arachnida: Opiliones). In: Smith AM editor. *Biological Adhesives*. Berlin: Springer.

Zatz C, Werneck RM, Macías-Ordóñez R, Machado G, 2011. Alternative mating tactics in dimorphic males of the harvestman *Longiperna concolor* (Arachnida: Opiliones). *Behav Ecol Sociobiol* **65**:995–1005.