Male dimorphism and alternative reproductive tactics in harvestmen
(Arachnida: Opiliones)

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Abstract

Strong sexual selection may lead small males or males in poor condition to adopt alternative reproductive tactics (ARTs) as a way to avoid the risk of being completely excluded from the mating pool. ARTs, sometimes accompanying morphological dimorphism among males, are taxonomically widespread, and especially common in arthropods. Here we review the current knowledge on ARTs and male dimorphism in a diverse but relatively overlooked group of arachnids, the order Opiliones, popularly known as harvestmen or daddy-long-legs. We begin with a summary of harvestman mating systems, followed by a review of the two lines of evidence for the presence of ARTs in the group: (1) morphological data from natural populations and museum collections; and (2) behavioral information from field studies. Despite receiving less attention than spiders, scorpions and insects, our review shows that harvestmen are an exciting group of organisms that are potentially great models for sexual selection studies focused on ARTs. We also suggest that investigating the proximate mechanisms underlying male dimorphism in the order would be especially important. New research on ARTs and male dimorphism will have implications for our understanding of the evolution of mating systems, sperm competition, and polyandry.

Key-words: alternative phenotypes, intrasexual dimorphism, female choice, phenotypic plasticity, polyandry, sexual conflict, sperm competition, weaponry

Introduction

Sexual selection is a powerful and pervasive evolutionary force in sexually reproducing species. Since male fitness is normally more influenced by mating success than female fitness (Bateman, 1948; Arnold & Duvall, 1994), males generally face stronger sexual selection than females. Through intersexual selection (female mate choice) and intrasexual selection (male-male competition), male mating success can become so biased that small males or males in poor condition face the risk of being completely excluded from the mating pool. Under such strong selective pressure, instead of fighting larger males or displaying to females, these small/poor condition males may adopt alternative reproductive tactics (ARTs; Oliveira et al., 2008). Once more than one mating tactic can be successfully employed by males, the scenario is set for the evolution of morphological divergence between males that employ different behaviors, usually through disruptive selection. The resulting discrete morphological variation has been termed male dimorphism (Gadgil, 1972), or more generally intrasexual dimorphism. A common pattern found in male dimorphic arthropods is that large males (hereafter majors) have more elaborate weaponry or ornaments, and usually guard females/territories or display to females, while small males (hereafter minors) have reduced or completely absent weaponry or ornaments, and usually sneak copulations, act as satellites, or even mimic females as a way to invade majors' territories (Thornhill & Alcock, 1983; Gross, 1996; Shuster & Wade, 2003; Oliveira et al., 2008).

Recent research has revealed that male dimorphism and its associated ARTs are widespread in animals, and seem to be especially common in arthropods. In insects, ARTs have been documented for over 200 species, from at least 11 orders and all major clades (reviews in Brockmann, 2008 and Buzatto et al., 2014a). In crustaceans, male dimorphism and some evidence for ARTs have been found in the classes Branchiopoda, Maxillopoda, and Malacostraca (Shuster, 2008). Although arachnids have a great diversity of reproductive

strategies (Thomas & Zeh, 1984), male dimorphism associated with ARTs has only been detected in two species of spiders (order Araneae; Clark & Uetz, 1993; Heinemann & Uhl, 2000), one pseudoscorpion (order Pseudoscorpiones; Zeh & Zeh, 2013), and a few species of mites (order Acari; Radwan, 1993, 1995, 2003) and harvestmen (order Opiliones; more on this order below). Male dimorphism has also been recently reported for a species of short-tailed whipscorpion (*Rowlandius potiguar*; Santos et al., 2013), but due to lack of behavioral data for the species, the existence of ARTs is still speculative in the order Schizomida.

As we intend to show here, an examination of the taxonomic literature reveals that male dimorphism is probably widespread in harvestmen, more than in any other major arachnid group. Unfortunately behavioral data on ARTs in this group are only available for a few species, all of them belonging to the family Gonyleptidae, which is exclusively distributed in the Neotropics (Kury & Pinto-da-Rocha, 2007). Species of this family present a high range of sizes (0.6-17 mm in body length and 2-185 mm in leg length), diverse coloration, as well as great variation in general shape and length of apophyses that are likely sexually selected (presenting strong sexual dimorphism) and may also function as defense mechanisms (Kury & Pinto-da-Rocha, 2007; Willemart et al., 2009; Pinto-da-Rocha et al., 2014). The reproductive behavior and mating systems of Gonyleptidae are also very diverse, including different forms of parental care and various mating strategies (Buzatto et al., 2013). In this study, we review the available morphological and behavioral evidence for ARTs in harvestmen, focusing mainly on gonyleptids, for which more information is available. We summarize our knowledge on the well studied species and use morphology to infer in which additional species ARTs are potentially present, setting promising targets for future research. Finally, we discuss the implications of ARTs for the reproductive biology and mating system evolution in the order Opiliones.

Harvestman mating systems

The order Opiliones comprises a diverse group of arachnids with nearly 6,500 species distributed in a great variety of terrestrial habitats, from tropical forests to deserts (Machado et al., 2007). Contrary to many animal groups, the reproductive behavior of harvestmen is better studied in the Neotropics than in any other part of the world. In a recent review, Buzatto et al. (2013) showed that 50.5% of the studies published on harvestmen reproduction from 1920 to 2012 were done in the Neotropics. They also showed that the number of studies published on the subject is accelerating in the Neotropical region since the 1990's, whereas this number has been fairly constant in temperate regions since the 1930's. Although there are several studies devoted to harvestmen reproductive biology, the current status of knowledge of their mating systems is fragmentary, and detailed field descriptions are still scarce. Two generalizations, however, can be made based on the available information. First, unlike most other arachnids, harvestmen are highly polygynandrous, so that both males and females engage in copulation with multiple mates throughout their lives (Machado & Macías-Ordóñez, 2007). Second, their mating strategies are highly diverse, but there seems to be a clear phylogenetic signal in the types of mating systems exhibited by the species of the four suborders.

The most likely mating system of species belonging to the suborders Cyphophthalmi and Dyspnoi, as well many species of the suborder Eupnoi, is scramble competition (Buzatto et al., 2013). Among these groups, which are mainly distributed in extra-tropical regions (Kury, 2013), females lay eggs on substrates that cannot be profitably monopolized by males, such as soil (Juberthie, 1972), the bark of trees, leaf litter (Edgar, 1971), cracks on rocky walls (Martens, 1969; Wijnhoven, 2011), and abundant snail shells (Pabst, 1953). Therefore, the spatial distribution of resources seems to play an important role in determining the type of mating system exhibited by different species (Buzatto et al., 2013). In several harvestman

species with scramble competition mating systems, males offer nuptial gifts to their mates. These nuptial gifts are glandular secretions produced either on the base of male's chelicerae and delivered directly to the female's mouth before copulation (Martens, 1969; Meijer, 1972) or on the base of the penis, where females feed during penetration (Macías-Ordóñez et al., 2010; Burns et al., 2013). Although males of these species may fight for the access to receptive females, there is no evidence that males defend them.

Although there are some records of resource and female defense polygyny in species of the suborder Eupnoi (Macías-Ordóñez, 1997, 2000; Wijnhoven, 2011), this type of mating system seems to be particularly common among species of the suborder Laniatores (Buzatto et al., 2013), which are mainly distributed in tropical regions. This is especially true for the highly diverse Gonyleptidae, in which males often fight each other for the possession of territories that are visited by females looking for oviposition sites. These reproductive territories include natural cavities on trunks and riverside banks (Machado et al., 2004; Nazareth & Machado, 2010), rocks (Zatz et al., 2011), specific host plants (Buzatto & Machado, 2008), and mud nests built by males (Mora, 1990). In some species, females remain inside the male's territory after oviposition, forming harems that may include more than ten females (Buzatto & Machado, 2008; Zatz et al., 2011). In other species, females abandon the male's territory after oviposition, leaving their eggs under the male's guard (Mora, 1990; Nazareth & Machado, 2010). Mate guarding is frequent among species exhibiting resource-defense polygyny, probably because the risk of female remating is relatively high (see below).

Alternative reproductive tactics in harvestmen

Morphological evidence

A simple first step to detect ARTs in any animal group is to investigate morphological variation among males of a population, looking for bimodalities in the size distributions and/or nonlinearity in the allometries of secondary sexual traits (Knell, 2009). The downside of this approach is that ARTs are not necessarily associated with morphological divergence between males that adopt different tactics, and in many cases males can switch between mating tactics over the course of their development, or repeatedly depending on fluctuating environmental conditions (examples in Oliveira et al., 2008). Therefore, lack of morphological divergence among males is not evidence for lack of ARTs, but the presence of this divergence hints to the existence of ARTs. As far as we know, there are no data to suggest that ARTs or male dimorphism exist in the suborders Cyphophthalmi or Dyspnoi, which together comprise approximately 530 species (Kury, 2013). On the other hand, morphological evidence for male dimorphism is abundant for the two most diverse suborders, Eupnoi and Laniatores, which together sum nearly 6,000 species (Kury, 2013).

In the Eupnoi, male dimorphism has been detected in at least three families. In the Protolophidae (genus *Protolophus*), majors and minors may present a two fold difference in the thickness of their pedipalps (Table 1). In the Neopilionidae, male chelicerae can be extremely enlarged, up to 23 times longer in majors than in females, and nearly five times longer in majors than in minors (Taylor & Hunt, 2009). Male chelicerae seem to be dimorphic in at least seven neopilionid species belonging to the genera *Spinicrus*, *Neopantopsalis*, and *Pantopsalis* (Table 1; Fig. 1A). A similar pattern of male dimorphic chelicerae elongation is also found in two species of Phalangiidae belonging to the genus *Rhampsinitus* (Table 1). Species of the genus *Zacheus* present great variation in chelicerae robustness, but it is not clear whether this variation is continuous or discrete (Šilhavý, 1965).

In the Laniatores, discrete variation in the size and/or robustness of male chelicerae has been described for scattered species in many families, including Biantidae, Epedanidae, Cosmetidae (Fig. 1B), and Stygnidae (Table 1). There are also anecdotal reports of ‘female-like’, ‘beta-males’, ‘effeminate males’ or ‘poecilandric males’ (potentially minors) in other families, in which male dimorphism is evident in other body parts. Among the Triaenonychidae, for instance, structures that may be intra-sexually dimorphic include the dorsal scute, chelicerae, pedipalps, and maxillary lobes of the second pair of pedal coxae (Forster, 1954; Table 1; Fig. 1C). Perhaps the most bizarre form of intra-sexual dimorphism occurs in *Roquettea singularis* (Cosmetidae), in which majors bear ‘basally fused and rounded’ protuberances on their dorsal scute, whereas minors bear less developed spines on their dorsal scute, similar to females (Ferreira & Kury, 2010; Table 1; Fig. 1D). Unfortunately, the potential function of these structures is a mystery. The most detailed quantitative morphological studies on male dimorphism in harvestmen are concentrated in the Gonyleptidae, which will be explored in more detail below.

There is a great variety of male weaponry across gonyleptid species, arising from protuberances on different parts of their bodies and on nearly every appendage (Kury & Pinto-da-Rocha, 2007). More often than not, these weapons are apophyses that grow from a given position on the animals’ carapace, or from one or more segments of their appendages, especially the fourth pair of legs. Sometimes the whole leg is extremely elongated and functions as a weapon (Buzatto & Machado, 2008; Zatz et al., 2011; Table 1). The degree to which males express these weapons can vary greatly within species, and the taxonomic literature on Gonyleptidae contains abundant evidence of male dimorphism (Table 1; Figs. 1E-F), suggesting the existence of ARTs. However, none of these studies presents statistically supported tests of male dimorphism, or appropriate sample sizes to investigate whether the variation in the sizes of males and/or their weapons is dimorphic or continuous (e.g., Kury,

2008; Mendes, 2011; Ázara et al., 2013). Below we elaborate on the few studies that conducted statistical tests to detect male dimorphism (cf. Rowland & Qualls, 2005 and Knell, 2009) in harvestmen.

One of the most evident diagnostic traits of harvestmen is the elongated and thin second pair of legs (also known as legs II), typically used as a tactile and chemical sensory organ (Machado et al., 2007). However, in most species of the subfamily Goniosomatinae, the second pair of legs is even further elongated, reaching the amazing length of 183 mm in *Mitogoniella taquara*, which is 22 times longer than the body (DaSilva & Gnaspini, 2009). This exaggerated male trait has been implicated in male-male fights (see below), and a few species of the subfamily show male dimorphism in the length of this structure (DaSilva & Gnaspini, 2009; Buzatto et al., 2011; Ázara et al., 2013). In *Serracutisoma proximum*, a species that inhabits the Atlantic Forest from south-eastern Brazil, two male morphs are clearly distinguishable on the basis of the relative length of the second pair of legs. From 6% to 37% of male *S. proximum* in natural populations do not show the exaggerated elongation of the second pair of legs that is characteristic of majors (Munguía-Steyer et al., 2012), and this is the first line of evidence for the existence of ARTs in the species. The mating tactic of this small male morph (hereafter ‘minors’) in *S. proximum* is in fact strikingly different to that of the conspecific majors, and will be discussed in detail below in the topic *Behavioral evidence*.

Exaggerated leg elongation is also common in the subfamily Mitobatinae. However, whereas the second pair of legs is still long, thin, and used as a sensory organ as in other harvestmen, it is the fourth pair of legs (also known as legs IV) that presents extreme degrees of elongation in this subfamily, reaching the extraordinary length of 185 mm in *Mitobates triangulus*, which is more than 37 times longer than the body (Pinto-da-Rocha & Giribet, 2007). High degree of leg elongation is the rule in Mitobatinae, but small males are typically incapable of producing these unique elongations. As a result, there is enormous intraspecific

variation in the length of the fourth legs in species of the subfamily, often resulting in male dimorphism (Buzatto et al., 2014b). Behavioural data on ARTs, though, is available for only one species of Mitobatinae, *Longiperna concolor* (see topic *Behavioral evidence*).

Further evidence that male dimorphism can be quite common in harvestmen comes from a recent study that systematically searched for these dimorphisms in 48 species of Gonyleptidae (Buzatto et al., 2014b). This study investigated two potentially sexually selected traits: the lateral apophysis on the coxa of the right fourth leg (C4A), and the femur of same leg (F4). These two traits are known to be employed in male fights in some species of the family (Buzatto & Machado, 2008; Nazareth & Machado, 2009, 2010; Willemart et al., 2009; Zatz et al., 2011). Buzatto et al. (2014b) found that C4A showed almost 30 times more variance (standardized by the means) among conspecific males than body size, and in 10 species (~21%) the distribution of this trait was significantly bimodal, resulting in male dimorphism (Table 1). Similarly, F4 showed up to 200 times more variance (standardized by the means) among conspecific males than body size, and its distribution was bimodal in nine species (~19%), constituting male dimorphism (Table 1). The study also showed that for both C4A and F4, sexual dimorphism is the most likely ancestral state in Gonyleptidae (Fig. 2). Moreover, male dimorphism in these two structures has been gained several independent times in the family, suggesting great evolutionary flexibility (Fig. 2).

Behavioral evidence

Since morphological analyses should only be considered the first step towards convincingly demonstrating the existence of ARTs (Knell, 2009), we now move on to presenting behavioral data on ARTs for three well-studied Neotropical species. The best behavioral evidence of ARTs in harvestmen comes from *S. proximum*. At the beginning of the reproductive season, majors of this species establish territories at river margins on certain

plant species that are used as oviposition sites. Majors defend these territories using their unusually elongated legs II in apparently ritualistic fights, in which both males completely extend these legs laterally (forming a 180° angle between the right and left leg), face each other, and repeatedly hit the tip of each others legs with the tips of their own legs (Buzatto & Machado, 2008). Occasionally, they may also attack each other with strikes of the pedipalps and chelicerae, which may explain why many adult males in the population have amputated limbs (Buzatto & Machado, 2008). Interestingly, these fights do not seem to be settled on the basis of leg length, and whether the behavior of hitting each other with legs II represents a battle of endurance (fights can last for over one hour) or functions in mutual assessment, is still unknown. The territories are visited by ovigerous females that copulate with majors, and lay their eggs on the under surface of the leaves (Buzatto et al., 2007). While the female oviposits, the major guards her with his long second pair of legs extended towards her, occasionally touching her legs and dorsum (Buzatto & Machado, 2008). During the mating season, which lasts from six to eight months, several females may mate with a major. These females stay in the major's territory guarding their eggs until they hatch, which may last 30-40 days (Buzatto et al., 2007). After the arrival of several females, majors concentrate their patrolling activity mostly on egg-guarding females, shifting the mating system to a female defense polygyny (Buzatto & Machado, 2008). The formation of these harems is probably the rule in the Goniosomatinae, with records for all genera except *Piatan* (B.A. Buzatto & G. Machado, unpublished data).

Besides territorial defense performed by majors, there is also an ART reported for minors of *S. proximum*, which have a short second pair of legs (see topic *Morphological evidence*). Minors never fight or patrol territories, but instead invade the territories of majors and furtively mate with egg-guarding females (Buzatto et al., 2011). This mating tactic is only possible because females may take up to 14 days to complete oviposition. Therefore,

although nearly 80–90% of the eggs are laid in the first 24 h after copulating with majors, minors can sire the remaining eggs if they successfully copulate with egg-guarding females in a two-week period after the beginning of oviposition. Minors can invade several harems in a single reproductive season, and around 70% of these invasions may lead to successful copulations (Buzatto et al., 2011). Considering that harvestmen are mostly tactile animals, unable to form images, minors may take advantage of perceptual limitations of majors in detecting intruders by visiting females in the periphery of their harems. In fact, an intruder cannot be detected by a major until physical contact is established, which has two important implications for harem invasions. First, as the number of females increases, it becomes more difficult for majors to successfully defend all of them inside their harem. Second, a minor can seize the opportunity to copulate with one or more females when the major is copulating or closely guarding another female of his harem (Munguía-Steyer et al., 2012).

Another species for which there is behavioral evidence of ARTs is *L. concolor*, which also inhabits the Atlantic Forest from south-eastern Brazil. In this species, majors have an extreme exaggeration in the fourth pair of legs in a clearly convergent adaptation to the kind of fights seen in Goniosomatinae. In *L. concolor*, fighting males turn around so that they are back to back, hold their fourth pair of legs laterally extended, and repeatedly hit each other with the tips of their legs (Zatz et al., 2011). The majors' mating tactic is based on resource defense, and they fight for the possession of oviposition sites at river margins, such as rocks and fallen trunks. These sites are visited by females that copulate with the territory owners and remain inside their territories during the entire breeding season forming harems. However, like other harvestman species in which females do not guard the offspring, *L. concolor* females produce eggs continuously, laying them individually on the substrate and covering them with debris (Zatz et al., 2011). Therefore, it is impossible for majors to monopolize all of the fertilizable eggs inside a harem, leaving room for invader males that

succeed in copulating with harem females to sire at least some offspring. These invasions in fact occur and are accomplished mostly by minors, which have a short fourth pair of legs and seem to rely on an ART. Minors are very mobile along the stream margins, rarely defend territories, and have never been observed fighting other males (Zatz et al., 2011).

Finally, we will describe what is known on the ARTs of *Zygopachylus albomarginis* (Manaosbiinae), a species that inhabits tropical forests in Panama. Males build cup-like mud nests that are used to attract females and are where they copulate and guard the eggs. Males also actively invest in repairing their nests and protecting them from invasion by conspecific males, as well as in defending the eggs against predation and fungal attack (Rodriguez & Guerrero, 1976; Mora, 1990). Although nests are necessary for males to obtain mates, not all males in the population build nests and many adult males can be found without a nest during the breeding season. Vagrant males can acquire a nest by occupying an empty one or by displacing the occupant of a defended nest. The frequency of nest takeovers varies during the breeding season and also among sites, suggesting that social and/or environmental factors play a role in males' behavior (Mora, 1990). Unfortunately, there is no information about whether this alternative form of acquiring a nest has morphological correlates among males. Moreover, males and females are barely distinguishable based on external morphology and, contrary to many gonyleptid species, they have no spine or tubercle that can be used as a weapon. Consequently, in this species we do not expect to find easily recognizable male morphs, as those reported for *S. proximum* and *L. concolor*. The existence of ARTs in *Z. albomarginis*, as well as other harvestman species exhibiting exclusive paternal care, certainly deserves further investigation.

Proximate causes of male dimorphism

Male dimorphism has been initially modeled under a dichotomy between genetic polymorphisms ('alternative strategies') and phenotypic plasticity ('conditional strategies'; Austad, 1984; Gross, 1996), but it has since been recognized that gene-by-environment (GxE) interactions play a role in most well-studied cases of male dimorphism (Emlen, 2008). In some systems, alternative male phenotypes are influenced by one or a few loci, and are expressed through Mendelian modes of inheritance. The expression of such genetic polymorphisms is not sensitive to environmental conditions, which has been supported in a few species of crustaceans (Shuster, 2008), damselflies (Tsubaki, 2003), birds (Krüger, 2008), fish (Taborsky, 2008), and lizards (Sinervo & Lively, 1996; Calsbeek & Sinervo, 2008). In harvestmen, the only evidence of a purely genetic polymorphism as the proximate mechanism for male dimorphism comes from *Protolophus tuberculatus* (Protolophidae), a species from California (Tsurusaki & Cokendolpher, 1990). Different number of chromosomes were found in males of different morphs (the major had 20, whereas the minor had 18), but only one individual of each morph was analyzed, and they were collected in different years (Tsurusaki & Cokendolpher, 1990). Therefore, further studies would be valuable to investigate the potential of chromosome number as a proximate mechanism for male dimorphism in harvestmen.

More commonly, however, male dimorphism is better understood as the result of a conditional strategy, reflecting a polyphenism, i.e., the differential expression of alternative phenotypes from a single genotype depending upon environmental conditions (West-Eberhard, 2003). In polyphenic dimorphisms, individuals' phenotypes are decided through conditional rules (Dawkins, 1980; Hazel et al., 1990). For instance, if status determines the fitness of a particular phenotypic tactic, alternative phenotypes may evolve status-dependent expression. Individuals with status higher than an evolutionarily stable switchpoint adopt

one phenotype, whilst individuals with status lower than this switchpoint adopt the other (Hazel et al., 1990; Gross, 1996). Such polyphenisms accommodate GxE interactions because genetic variation is known to underlie the sensitivity to the environment, such that the switchpoints themselves can be understood as polygenic traits (Hazel et al., 1990; Tomkins & Hazel, 2007; Buzatto et al., 2014c) with complex patterns of inheritance (Buzatto et al., 2012a,b).

Polyphenic male dimorphism raises questions about the kind of developmental mechanisms that can allow individuals to adopt alternative phenotypes, and how environmental cues trigger developmental dichotomy (Nijhout, 1999). In all arthropods that are known to have a developmental mechanism of polyphenic regulation, the expression of different male phenotypes has been found to be regulated by hormones (Nijhout, 2003; Hartfelder & Emlen, 2011; Emlen et al., 2012). Developmental hormones are directly regulated by (or are themselves) neurosecretory factors and the hormonal regulation of development is under the control of the central nervous system (Nijhout, 1994). As a consequence, the central nervous system can integrate information about the animal's internal and external environment and use this information to regulate the secretion of hormones, allowing development to respond to a wide diversity of environmental signals (Nijhout, 2003). These environmental cues can consist of photoperiod, temperature, pheromones, crowding, and changes in food quality or quantity (Nijhout, 1999; Buzatto et al., 2014a).

There is no study specifically focused on the proximal causes of male dimorphism in harvestmen, probably because the time from egg-hatching to adulthood in Laniatores (the most intensively studied suborder) may last from 6 to 12 months (Gnaspini, 2007). Morphological studies on *S. proximum* and *L. concolor*, however, provide some clues on the subject (Buzatto et al., 2011; Zatz et al., 2011). For both species, the static allometry of their

sexually dimorphic legs indicates that major phenotype expression depends on body size, which shows a clear unimodal distribution (see Fig. 5.4 in Buzatto et al., 2013). This scenario suggests a polyphenism in which males' body size is determined by environmental factors, resulting in a normal distribution, whereas males' morph is at least partially determined by body size. Moreover, for both harvestman species there is a significant overlap in the body sizes of male morphs, which can be partially explained by variation among individual genotypes in the position of the switchpoint determining the body size that needs to be achieved for the major phenotype to be expressed (Tomkins & Hazel, 2007). At least for *S. proximum*, the variation in the distribution of switchpoints was estimated to be large, suggesting that selection on this trait has probably been weak in the population's recent history (Buzatto et al., 2011). In favor of this suggestion, results from a long-term mark-recapture study showed that major phenotype expression does not result in survival costs, so that a small male that expresses the major phenotype should not be severely penalized by this decision – at least in terms of survival (Buzatto et al., 2011).

Despite the paucity of information on the proximate causes of male dimorphism in Opiliones, Hunt (1979) found a strong ecological effect underlying the expression of the two male morphs of *Equitius doriae* (Triaenonychidae), a species from southeastern Australia. Individuals of this species go through a dormant stage during winter, and most males overwinter as fifth instar nymphs, reaching adulthood in spring and early summer. However, up to 37% of males overwinter as fourth instar nymphs, or even at earlier instars, reaching adulthood in summer and early autumn, and possessing less developed secondary sexual traits. Interestingly, these males are more common in drier habitats (Hunt, 1979), probably due to lower growth rates caused by resource scarcity in such habitats. *Equitius doriae* is, therefore, a good candidate for controlled experiments under laboratory conditions to investigate the role of food availability on growth rate and ultimately on the expression of

different male morphs. This approach has already been used for other arthropod species and it is an important first step toward a more comprehensive understanding of the genetic and environmental factors underlying polyphenic male dimorphism in harvestmen (e.g., Moczek & Emlen, 1999; Tomkins, 1999).

Regardless of the proximate mechanisms leading to two male morphs in harvestmen, a recent comparative study including 48 species of Gonyleptidae has shown that male dimorphism never occurred in sexually monomorphic species (Buzatto et al., 2014b). Considering that the authors compared females of male dimorphic species with only majors, this result suggests a correlation between sexual and male dimorphism in harvestmen. A similar study on dung beetles also showed a tight correlation between the two types of dimorphism (Emlen et al., 2005), and used this correlation to support the idea that the endocrine threshold mechanism that switches horn growth on and off during development is present in minors and in females of all sizes (Emlen et al., 2006; Shingleton et al., 2007). Contrary to dung beetles, harvestmen do not go through metamorphosis, and their developmental pathway from nymphs to adults is very different from that of holometabolous insects (Truman & Riddiford, 2002; Minelli, 2003; Gnaspini, 2007). Therefore, the findings reported for harvestmen indicate that the specific endocrine threshold mechanism present in dung beetles (and potentially in other male dimorphic holometabolous insects) is not a necessary condition for the correlated evolution of sexual and male dimorphism in general. The correlation between the two types of dimorphism in harvestmen could more generally be the result of selection acting against secondary sexual traits in females and small males, generating intralocus sexual conflict (Rice & Chippindale, 2001) and intralocus tactical conflict among males of different status (West-Eberhard, 2003; Morris et al., 2013) at the same time (Buzatto et al., 2014b). Investigating the proximate mechanisms in small males and in females of sexually and male dimorphic harvestmen is a

promising avenue for better understanding the coevolution of such dimorphisms in non-holometabolous arthropods.

Consequences for sexual selection

Female mate choice and sexual conflict

The freedom females have to choose their mates is partially determined by the type of male-female associations (Borgia, 1979). In resource defense polygynous mating systems, females can only access essential resources by mating with the males controlling them (Emlen & Oring, 1977). In this situation, females may actively choose mates based on the phenotypic attributes of resource-owning males, including body or weapon size, conspicuousness of ornaments, composition or concentration of pheromones, or rates of sexual displays. Females may also choose mates indirectly, because oviposition site selection promotes male-male competition for the possession of preferred sites, thus increasing females' chance of mating with successful competitors (Wiley & Poston, 1996). Although poorly explored, indirect female choice is likely to occur in harvestmen exhibiting resource defense polygyny. Females of *S. proximum*, for instance, show marked preference for certain plant species, which represent predictable resources searched by females at the time of breeding (Buzatto & Machado, 2008). As we exposed above, majors monopolize territories containing the preferred plants to secure mates, and use their second pair of legs as weapons in fights for the possession of these territories. Therefore, the positive correlation between male second leg length and harem size reported for this harvestman species may emerge as a consequence of two non-mutually exclusive processes. First, females that visit different territories may benefit from actively preferring males with longer legs, assuming this trait indicates male quality. Second, because majors are under intense intra-sexual competition (Fig. 3), the possession of a territory may work as an honest signal of male quality. Therefore,

females that passively prefer to mate with territory-owning males avoid any potential assessment costs, and still benefit from producing offspring fathered by the best competitors (Buzatto & Machado, 2008).

While sexual selection theory considers both male-male competition and female mate choice as important selective pressures in the evolution of the major tactic, only male-male competition is traditionally considered to act on the minor tactic (Taborsky et al., 2008). Female preference is acknowledged to produce disruptive selection among males only when a polymorphism in female choice selects for a polymorphism among males (Kawase & Nakazono, 1996; Taborsky, 2008). However, female mate preference for minors may have an important role in the evolution of ARTs (Luttbeg, 2004; Neff, 2008; Morris & Ríos-Cardenas, 2013). In fact, studies with fish show that females may even prefer to mate with minors (commonly referred to as ‘parasitic males’ in fish), probably because majors (commonly referred to as ‘bourgeois males’ in fish) control access to many females and may be thus sperm limited (e.g., Hugie & Lank, 1997; Harris & Moore, 2005; Reichard et al., 2007). Although ovigerous females of *S. proximum* are constrained to copulate with majors to gain access to oviposition sites, egg-guarding females promptly accept copulation with minors that manage to invade territories (Buzatto et al., 2011). Moreover, contrary to some fish, frog, and toad species (Taborsky, 2008; Zamudio & Chan, 2008), minors of *S. proximum* apparently do not need to force copulations. The opportunity to copulate with minors may increase female fertility if majors are either sperm limited or have alleles that are incompatible with their mates (Zeh & Zeh, 1996, 1997; Fig. 3). By mating polyandrously, females may also increase genetic diversity within their clutches (Yasui, 1998; Fig. 3).

Given the multiple possible benefits of polyandry in *S. proximum*, we suggest that females’ retention of non-fertilized eggs in their reproductive tract after copulation with territory-owners has evolved as a tactic to overcome majors’ monopoly and gain the

452 opportunity to mate with additional males (Buzatto et al., 2011; Fig. 3). According to this
453 hypothesis, sexual conflict between females and majors would be a key component to
454 understand the evolution and maintenance of ARTs (see discussion in Alonzo, 2008).
455 Alternatively however, it is possible that females of *S. proximum* do not retain non-fertilized
456 eggs, but rather lay all mature eggs after copulation with territory owners, and then continue
457 to produce more eggs at a slower rate while guarding the first clutch. The key to distinguish
458 between these two hypothesis in the future would be to dissect females right after they lay
459 the first large clutch of eggs, and check whether they have mature (but non-fertilized eggs) in
460 their reproductive tract.

461   Although poorly explored, conflict could also emerge between females and minors of
462 *S. proximum*. A field experiment has shown that at least some majors temporarily care for
463 clutches that were left unattended in their harems. Natural cases of temporary male care
464 have also been recorded in the field, probably because egg-guarding females deserted or
465 died (Buzatto & Machado, 2009). Temporary male care may be important for offspring
466 survival (and hence female fitness) because egg predators can consume entire clutches in a
467 few hours or days (Buzatto et al., 2007). If the propensity of a major to temporarily care for
468 an unattended clutch is influenced by his certainty of paternity, conflict between females and
469 minors will exist (Fig. 3). We are currently investigating this question, and preliminary
470 results indicate that certainty of paternity indeed affects the propensity of parental care by
471 majors. The frequency of temporary male care was higher when clutches were recently laid
472 (Alissa et al., 2013), probably because mate-guarding is more intense in the 2-4 days after
473 oviposition, and this behavior is highly effective in preventing sneak copulations (Buzatto &
474 Machado, 2008).

476 *Sperm competition*

477   Most harvestman females mate polyandrously, creating the opportunity for the sperm
478 of two or more males to coexist in the female's reproductive tract and thus compete for
479 fertilization of ova (Macías-Ordóñez et al., 2010). Sperm competition is widely recognized as
480 an important source of intrasexual conflict that modulates the total strength and direction of
481 sexual selection (Kvarnemo & Simmons, 2013; Fig. 3). In species exhibiting ARTs, minors are
482 constantly subject to sperm competition, since they usually mate with already mated
483 females. Majors, on the other hand, are subject to sperm competition only when minors
484 invade their harems (Parker, 1990). Sperm competition theory predicts that ejaculate
485 investment should increase with increasing sperm competition, and we should therefore
486 expect an asymmetry in ejaculate investment between morphs, with minors normally having
487 higher relative testis mass than majors. However, if minors are too common or too effective
488 in acquiring copulations, majors will also regularly face sperm competition, and the
489 asymmetry in sperm competition disappears. In this situation, the prediction is that no
490 difference in testes size between male morphs should be found (Parker, 1990; Simmons,
491 2001).

492   Munguía-Steyer et al. (2012) investigated how the relative frequency of minors (a
493 proxy of sperm competition intensity faced by majors) influences the relative gonadal
494 investment of majors and minors of *S. proximum* in 10 natural populations. Male dimorphism
495 was found to be ubiquitous in all populations, but there was no relationship between
496 gonadal investment, male morph, and relative frequency of minors across populations.
497 According to field observations conducted in one of the studied populations, more than 80%
498 of majors experienced some level of sperm competition, despite the fact that minors
499 composed only 20% of males (Buzatto et al., 2011). Moreover, some minors invaded multiple
500 harems, and most of the invasions resulted in copulations (Buzatto et al., 2011). Based on

these data, Munguía-Steyer et al. (2012) suggested that even a small relative frequency of minors in the population could greatly increase sperm competition faced by majors, which would explain the similarity in gonadal investment between morphs. They also proposed that sperm competition faced by majors would be more variable than that faced by minors because the probability of harem invasion by minors was positively related to harem size (Munguía-Steyer et al., 2012). Therefore, majors holding large harems would be under more intense sperm competition than majors holding small harems.

To test the hypotheses presented above, we used a sexual network approach in which males and females were connected by copulations (Muniz et al., in prep.). According to this approach, each individual may be characterized by its number of connections (i.e., sexual interactions) and by the number of connections of its mating partners, which brings information about sperm competition intensity. Our results support the prediction that minors face, on average, higher levels of sperm competition than majors and that sperm competition intensity is more variable among majors. Unexpectedly, however, majors owning large harems faced less intense sperm competition than owners of small harems, suggesting that sperm competition can be diluted among females in large harems (Muniz et al., in prep.). The meaning of this finding is twofold. First, the mean paternity attained by a territory owner should increase as harem size increases, which contrasts with the pattern reported for some mammals, in which males holding the largest harems do not have the highest reproductive success (e.g., Kaseda & Khalil, 1996; Heckel et al., 1999). Second, if majors holding small harems are also the ones losing more fertilizations to minors, the presence of the alternative tactic in *S. proximum* may increase the opportunity for sexual selection among males. Thus, although the presence of ARTs allegedly decreases the opportunity for sexual selection on males because the number of completely unsuccessful males decreases (Jones et al., 2001; Shuster & Wade, 2003), the influence of the minor tactic

on the opportunity for sexual selection can follow different directions, depending on which females these minors copulate with (McDonald et al., 2013).

Concluding remarks

Our review indicates that male dimorphism and ARTs are probably common among harvestmen, especially among species of the suborders Eupnoi and Laniatores, which comprise over 90% of the diversity in the order Opiliones. A comparative study with the Neotropical family Gonyleptidae clearly indicates that male dimorphism has evolved several times independently, pointing to the high lability of this trait. Although the precise developmental mechanisms that allow males to adopt alternative phenotypes in harvestmen are unknown, allometric studies suggest a polyphenism in which male body size is determined by environmental factors and male morph is partially determined by body size. Future research with harvestmen should focus on the role of genetic, endocrine, and environmental factors for morph determination because this data are pivotal for our comprehension of the proximate causes for the evolution of male dimorphism in the group. Additionally, detailed behavioral information on a wider set of species belonging to different families could reveal a great diversity of ARTs in the order. Our current knowledge on a single well-studied species clearly shows that interactions within and between sexes are complex and can bring novel insights into the role of sexual selection in maintaining alternative tactics in populations, which in turn affect mate choice, sexual conflict, sperm competition, and other key topics in sexual selection. We hope, therefore, that this review stimulates behavioral ecologists to develop interest for harvestmen, a fascinating group of organisms that offers unique opportunities to study ARTs and their fitness consequences.

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901 **Table 1.** List of harvestman species exhibiting male dimorphism. Species for which there is
902 behavioral information demonstrating the presence of alternative reproductive tactics are
903 marked with an asterisk. Observational evidence of intrasexual dimorphism includes verbal
904 statements of discrete male polymorphism in taxonomic studies, and statistical evidence
905 includes formal analytical tests indicating bimodalities in the size distributions and/or
906 nonlinearity in the allometries of secondary sexual traits. Although comprehensive, this list
907 is not exhaustive because we did not search all the taxonomic literature of the order
908 Opiliones.
909

Taxon	Main form of intra-sexual dimorphism	Type of evidence	Reference
EUPNOI: Neopilionidae			
<i>Neopantopsalis pentheter</i> , <i>N. psile</i> , and <i>N. quasimodo</i>	Length of chelicerae and spines on femur I	Observational	Taylor & Hunt, 2009
<i>Pantopsalis albipalpis</i> , <i>P. cheliferoides</i> , <i>P. coronata</i> , <i>P. johnsi</i> , <i>P. listeri</i> and <i>P. phocator</i>	Shape and length of chelicerae	Observational	Taylor, 2004, 2013a
<i>Megalopsalis minima</i>	Length of chelicerae and presence of a spine row on leg I	Observational	Kauri, 1954; Taylor 2013b
<i>Megalopsalis caeruleomontium</i> and <i>M. nigricans</i>	Length and armature of chelicerae	Observational	Taylor 2013b
EUPNOI: Phalangiidae			
<i>Phalangium opilio</i> (Japanese population)	Length of chelicerae and pedipalps	Observational and statistical	Tsurusaki & Takenaka, 2010
<i>Rhampsinitus leighi</i> and <i>R. telifrons</i>	Length of chelicerae	Observational	Staręga, 2009
EUPNOI: Protolophidae			
<i>Protolophus tuberculatus</i>	Thickness of pedipalps	Observational	Tsurusaki & Cokendolpher, 1990

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LANIATORES: Assamiidae			
<i>Metamermerus speculator</i>	Size of chelicerae	Observational	Forster, 1955
LANIATORES: Biantidae			
<i>Caribbiantes</i> sp.	Size and robustness of chelicerae	Observational	Pérez, 2000
LANIATORES: Cosmetidae			
<i>Arucillus armasi</i>	Size and robustness of chelicerae	Observational	Pérez González & Vasconcelos, 2003
<i>Cynorta vestita</i>	Size of chelicerae	Observational	Gnaspini et al., 2004
<i>Roquettea singularis</i>	Shape and size of tubercles in the dorsal scute	Observational	Ferreira & Kury, 2010; Kury & Ferreira, 2012
LANIATORES: Cranaidae			
<i>Santinezia manauara</i>	Size of the ventral apophyses on coxa IV	Observational	Gnaspini et al., 2004
LANIATORES: Epedanidae			
<i>Epedanellus tuberculatus</i>	Size of chelicerae	Observational	N. Tsurusaki, unpubl. data
<i>Heterobiantes insulanus</i>	Size of chelicerae	Observational	Suzuki, 1973
<i>Zepedanulus ishikawai</i>	Size of chelicerae	Observational	Suzuki, 1973
<i>Tokunosia tenuipes</i>	Size of chelicerae	Observational	Suzuki, 1973
<i>Pseudobiantes japonicus</i> *	Size of chelicerae	Observational	Suzuki, 1973; Tsurusaki & Fujikawa, 2004
LANIATORES: Gonyleptidae			
<i>Acrogonyleptes rhinoceros</i>	Size of the apophyses on coxa IV	Statistical	Buzatto et al., 2014b
<i>Arthrodes xanthopygus</i>	Size of the apophyses on coxa IV	Statistical	Buzatto et al., 2014b
<i>Cobania picea</i>	Size of the apophyses on coxa IV and length of femur IV	Statistical	Buzatto et al., 2014b
<i>Goniosoma varium</i>	Size of the apophyses on coxa IV	Statistical	Buzatto et al., 2014b
<i>Goniosoma venustum</i>	Size of the apophyses on coxa IV	Statistical	Buzatto et al., 2014b
<i>Gonyleptellus cancelatus</i>	Length of femur IV	Statistical	Buzatto et al., 2014b
<i>Heteromitobates discolor</i>	Size of the apophyses on coxa IV	Statistical	Buzatto et al., 2014b
<i>Heteropachylus inexpectabilis</i>	Size of the apophyses on		Mendes, 2011

	coxa and femur IV		
<i>Ischnoterus tenebrosus</i>	Length of femur IV	Statistical	Buzatto et al., 2014b
<i>Longiperna concolor</i> *	Length of leg IV	Statistical	Zatz et al., 2011; Buzatto et al., 2014b
<i>Megapachylus grandis</i>	Size of the apophyses on coxa and femur IV	Observational	Pinto-da-Rocha et al., 2012
<i>Mitogoniella mucuri</i>	Armature of leg IV and length of leg II	Observational	Ázara et al., 2013
<i>Multumbo dimorphicus</i>	Armature of leg IV	Observational and statistical	DaSilva & Kury, 2007; Buzatto et al., 2014b
<i>Neoancistrotus gracilis</i>	Length of femur IV	Statistical	Buzatto et al., 2014b
<i>Neosadocus maximus</i>	Size of the apophyses on coxa IV	Statistical	Buzatto et al., 2014b
<i>Progonyleptoidellus striatus</i>	Size of the apophyses on coxa IV	Statistical	Buzatto et al., 2014b
<i>Promitobates bellus</i>	Size of the apophyses on coxa IV and length of femur IV	Statistical	Buzatto et al., 2014b
<i>Promitobates ornatus</i>	Length of femur IV	Statistical	Buzatto et al., 2014b
<i>Ruschia maculata</i>	Length of femur IV	Statistical	Buzatto et al., 2014b
<i>Serracutisoma proximum</i> *	Length of legs II and IV	Statistical	Buzatto et al., 2011, 2014b
<i>Soaresia forficula</i>	Size of the apophyses on coxa and femur IV, size and shape of the apophyses on tergite III	Observational	Kury, 2008
LANIATORES: Kimulidae			
<i>Kimula cokendolpheri</i>	Presence of tubercles and apophyses on femur IV	Observational	Pérez, 1998
LANIATORES: Stygnidae			
<i>Stygnoplus tuberculatus</i>	Size and robustness of chelicerae	Observational	Pérez, 2000
<i>Stygnus brevispinis</i>	Size of chelicerae	Observational	Gnaspini et al., 2004
LANIATORES: Triaenonychidae			
<i>Equitius</i> (all species except <i>E. formidabilis</i>)	Size, robustness and armature of pedipalps	Observational (statistical for <i>E. doriae</i>)	Forster, 1955; Hunt, 1979, 1985
<i>Nuncia</i> (<i>Corinuncia</i>) <i>coriacea</i> ,	Size, robustness and	Observational	Forster, 1954

<i>N. (Corinuncia) smithi</i> , <i>N. (Corinuncia) stewartia</i> , <i>N. (Corinuncia) variegata</i> , <i>N. (Micronuncia) roeweri</i> , <i>N. (Nuncia) paucispinosa</i> , <i>N. (Nuncia) tumula</i> , <i>Hedwiga manubriata</i>	armature of pedipalps		
	Size, robustness and armature of pedipalps	Observational	Forster, 1954
<i>Nunciella kangarooensis</i>	Size, robustness and armature of pedipalps	Observational and statistical	Hunt, 1971
<i>Larifuga calcarata</i>	Size, robustness and armature of pedipalps	Observational	Kauri, 1961
LANIATORES: Zalmoxidae			
<i>Pachylicus hirsutus</i>	Length of leg IV	Observational	Goodnight & Goodnight, 1983
<i>Zalmoxis furcifer</i>	Length of leg IV	Observational	Sharma, 2012

FIGURE LABELS

Figure 1. Examples of male dimorphism in harvestmen. The most conspicuous dimorphic structures in all species are highlighted in dark grey. Leg insertions are represented in light grey. (A) Lateral view of *Pantopsalis phocator* (Neopilionidae) showing two morphs that differ in relation to the enlargement and broadness of their chelicerae (modified from Taylor, 2004). (B) Lateral view of *Arucillus armasi* (Cosmetidae) showing two male morphs that differ in relation to the robustness of their chelicerae (modified from Pérez González & Vasconcelos, 2003). (C) Lateral view of *Nuncia roeweri callida* (Triaenonychidae) showing two male morphs that differ in relation to the size and robustness of their paedipalps (modified from Forster, 1954). (D) Lateral view of *Roquettea singularis* (Cosmetidae) showing two male morphs that differ in relation to the format of a very large tubercle on the dorsal scute (modified from Kury & Ferreira, 2012). (E) Dorsal view of *Cobania picea* (Gonyleptidae) showing two male morphs that differ in relation to length of a large apophysis on the coxa of the fourth pair of legs. (F) Dorsal view of *Longiperna concolor* (Gonyleptidae) showing two male morphs that differ in relation to the length of the femur of the fourth pair of legs (modified from Pinto-da-Rocha & Bragagnolo, 2010). Scale bars: (A) 2 mm, (B-D) 1 mm, (E) 5 mm, (F) 3 mm.

Figure 2. Evolutionary history of sexual and male dimorphism in 48 species of gonyleptid harvestmen (adapted from Buzatto et al. 2014b). The traits used in this analysis were the length of the apophysis on the fourth coxa (C4A) and the length of the fourth femur (F4), both of which are potentially sexually selected traits that are used as weapons in male fights of at least some species in the family. For the sources of phylogenetic information, see the Supporting Information from Buzatto et al. (2014b). The history of transitions in sexual and male dimorphisms was reconstructed through parsimony, and the states are color coded as:

sexually and male monomorphic (state 0, white); sexually dimorphic and male monomorphic (state 1, gray); and sexually and male dimorphic (state 3, black). Information on C4A dimorphisms is not available for *Promitobates ornatus*. Sexual dimorphism is clearly the ancestral state for C4A, and probably for F4 as well. Male dimorphism, on the other hand, is probably derived (certainly so for C4A), and seems to have evolved several independent times in sexually dimorphic clades of Gonyleptidae.

Figure 3. Conflicts within and between the sexes in the harvestman *Serracutisoma proximum* (inspired by Fig. 18.4 in Alonzo, 2008). While females may derive indirect benefits from mating polyandrously with minors, majors' fitness increases if they have exclusive access to all fertilizable gametes inside their harems. This is the most important conflict between females and majors. Considering that the propensity of a major to temporarily care for an unattended clutch is influenced by his certainty of paternity, conflict between females and minors will also exist. Majors are in competition with other majors for the possession of territories containing the preferred plants used for oviposition and also for access to mates. Finally, minors are in conflict with majors and also with other minors for the access to the unfertilized eggs retained by females in their reproductive tract after the first oviposition bout.

FIGURE 1

FIGURE 2

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FIGURE 3

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