CHAPTER FOUR

Pre-copulatory and copulatory courtship in male-dimorphic arthropods

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Contents

1. Introduction

Sexual selection is a powerful and pervasive selective force in nature, which in most species acts more strongly on males than on females (Dewsbury, 2005; Janicke, Häderer, Lajeunesse, & Anthes, 2016). The difference in the intensity of sexual selection acting on each sex has several consequences, such as the evolution of male–biased sexual size dimorphism,

male weaponry, and male ornaments (Andersson, 1994). These sexually selected traits are employed in agonistic interactions between males for direct or indirect access to females and/or in courtship displays to females (reviewed in Berglund, Bisazza, & Pilastro, 1996 and McCullough, Miller, & Emlen, 2016). Large males, with exaggerated weapons or ornaments, usually have access to more females than smaller males, which have poorly developed weapons or ornaments (examples in Andersson, 1994 and Clutton-Brock, 1988). When females mate mainly with a subset of males showing exaggerated sexually selected traits, there is an opportunity for the evolution of alternative reproductive tactics (ARTs), defined as a form of mate acquisition used by some males (often with distinct phenotypes) that differs from the prevailing (or simply most conspicuous) form of mate acquisition exhibited by other males in the population (Gross, 1996; Shuster & Wade, 2003; Taborsky, Oliveira, & Brockmann, 2008).

In many animal species, large males with exaggerated weaponry or ornaments exhibit a reproductive tactic that relies mostly on guarding females, monopolizing resources, and/or exhibiting elaborate sexual displays (Taborsky et al., 2008). Because large males tend to win fights and females usually prefer males with the most elaborate ornaments, pre-copulatory sexual selection favors males with the highest values of sexually selected traits. In turn, small males with reduced or completely absent weaponry or ornaments rely on ARTs that rarely involve male-male aggression or elaborate pre-copulatory displays. Instead, they sneak copulations, act as satellites, or even mimic females to invade territories or harems guarded by large males (examples in Oliveira, Taborsky, & Brockmann, 2008). In most of these cases, small body size and inconspicuousness increase male mating success, so that pre-copulatory sexual selection favors males with the lowest values of sexually selected traits. Whenever two reproductive tactics with different phenotypic optima are successfully employed by males in a population, disruptive selection acts against males with average values of sexually selected traits and favors males in both extremes of the phenotypic distribution. The disruptive selection regime leads to the evolution of *intrasexual male dimorphism* or simply *male dimorphism*, which implies the presence of two discrete male morphs in the same population (Gadgil, 1972; Gross, 1996; Taborsky et al., 2008).

Male dimorphism associated with ARTs has been reported for several taxa, but it seems to be especially common among terrestrial arthropods (Fig. 1), with numerous examples in insects (reviewed in Brockmann, 2008 and Buzatto, Tomkins, & Simmons, 2014) and arachnids, particularly
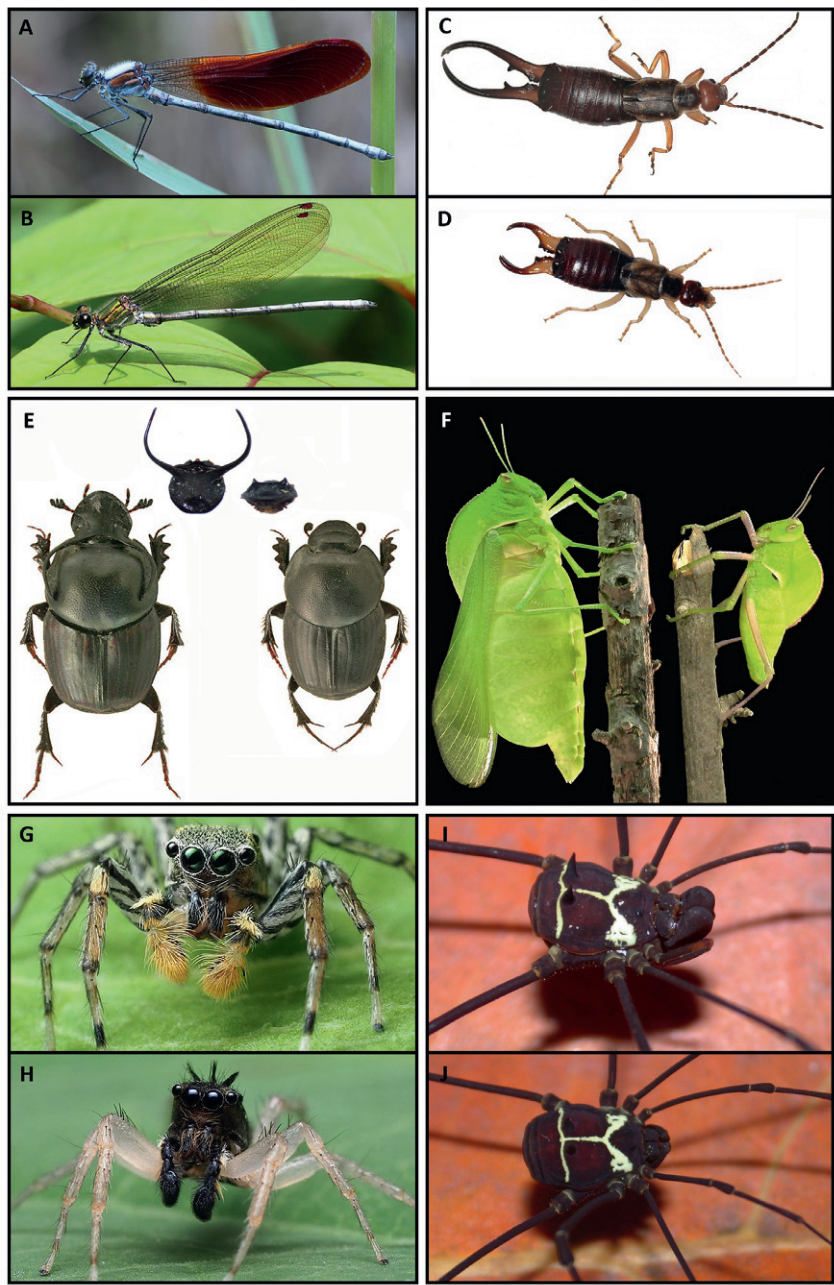
Fig. 1 See figure legend on next page.

those belonging to the order Opiliones, commonly known as harvestmen (Buzatto & Machado, 2014). In the last 40 years, we accumulated much information on morphological differences between male morphs in insects (Buzatto et al., 2014) and arachnids (Buzatto & Machado, 2014). In some species of insects and mites, we also understand the proximate mechanisms (genetic and physiological) that lead to the morphological differences between morphs (e.g., Emlen, 2008; Radwan, 2009). In both insects and arachnids, we know how reproductive tactics differ between morphs (Brockmann, 2008; Buzatto & Machado, 2014) and how different reproductive tactics translate into differences in mating success (e.g., Alcock, 1996a; Muniz, Guimarães, Buzatto, & Machado, 2015; Watanabe & Taguchi, 1990). Finally, terrestrial arthropods have been used as model systems to test theoretical models on how sperm expenditure should differ between male morphs (reviewed in Kustra & Alonzo, 2020 and Simmons, 2001).

Despite the advances mentioned above, for most male-dimorphic species of insects and arachnids we have little information on how males and females interact both before and during copulation. With only few exceptions, we do not know whether pre-copulatory and copulatory courtship differ between male morphs. We know, however, that pre-copulatory courtship is a key component of male mating success, and that copulatory courtship has great impact on the fertilization success of many species of terrestrial arthropods (examples in Peretti & Aisenberg, 2015 and Thornhill & Alcock, 1983). Given that male morphs are under different sexual selection regimes and face different costs and challenges associated with mating acquisition and fertilization (Brockmann & Taborsky, 2008; Gross, 1996; Parker, 1990), it would be expected that they also differ qualitatively and quantitatively in pre-copulatory and copulatory courtship behaviors. Here, we first conduct

Fig. 1 Examples of male-dimorphic arthropod species included in our review: the damselfly *Mnais costalis*, with an (A) orange-winged morph and a (B) clear-winged morph; the earwig *Forficula auricularia*, with a (C) large morph bearing long forceps and a (D) small morph bearing short forceps; (E) the dung-beetle *Onthophagus taurus*, with a large and horned morph and a small and hornless morph; (F) the bladder grasshopper *Bullacris membracioides*, with a large and winged morph and a short and wingless morph; the jumping spider *Maevia inclemens*, with a (G) stripped morph and a (H) tufted morph; the harvestman *Paecilaemula lavarrei*, with a (I) large morph bearing powerful chelicerae and a (J) small morph bearing delicate chelicerae. Photos by: (A and B) Alpsdake, Wikipedia Commons; (C) BartBotje, Wikipedia Commons; (D) EugeneZelenko, Wikipedia Commons; (E) Lech Borowiec (bodies) and Bruno A. Buzatto (heads); (F) Moira J. van Staaden; (G and H) Spidereyes, Wikipedia Commons; (I and J) Glauco Machado.

a systematic review of the literature on male dimorphism in terrestrial arthropods to identify studies that provide comparisons of pre-copulatory and/or copulatory courtship behaviors between male morphs. Then, we summarize the behavioral information we found in our review, calling attention to general patterns. Based on these patterns, we propose four main processes that may explain the differences reported so far between male morphs in their pre-copulatory courtship. We also propose hypotheses on how and why copulatory courtship should differ between male morphs, and the implications of this difference for the evolution of male genitalia. Finally, we present the most important gaps in our knowledge and indicate directions for future studies on pre-copulatory and copulatory courtship in terrestrial arthropods exhibiting male dimorphism coupled with ARTs.

2. Systematic review

To have a general picture of what is currently known about male-female sexual interactions in terrestrial arthropods exhibiting male dimorphism coupled with ARTs, we conducted a systematic review based on the PRISMA protocol (Preferred Reporting Items for Systematic Reviews and Meta-Analyses, see http://www.prisma-statement.org/). First, we searched for information in three pre-existing reviews on ARTs in insects and arachnids. Brockmann (2008) and Buzatto et al. (2014) are two extensive reviews on ARTs in insects that indicate when each male reproductive tactic has a morphological correlate. Buzatto and Machado (2014) is a review on male dimorphism in harvestmen that also includes many cases of male dimorphism in other arachnid orders, such as spiders, pseudoscorpions, mites, and short-tailed whip scorpions. From these three reviews, we selected only the species indicated as exhibiting male dimorphism, so that species exhibiting continuous variation in sexually selected male traits were not included here. Then, we read the original articles (duplicates removed), searching for any information about pre-copulatory and copulatory courtship behaviors of each morph (Fig. S1 in Supplementary Material in the online version at https://doi.org/10.1016/bs.asb.2022.01.002).

Once we had a list of selected papers obtained in the literature search described above, we performed a forward search in *Google Scholar*, searching for articles that cited the papers in our list. In this forward search, we looked for articles that contained information about pre-copulatory and copulatory courtship behaviors in insects and arachnids with discrete male morphs. We read the title, abstract, and keywords of the articles found in the forward

search and, in cases when it was not clear if the study contained information about pre-copulatory and copulatory courtship behaviors, we also searched the whole text for the following keywords: "court" (which includes the word "courtship"), "mate," "mating," and "copula" (which includes the word "copulation"). When we found the necessary information, or at least an indication that the article could be useful, we proceeded to full reading.

Finally, we searched the *Web of Science* and *Scopus* databases for a combination of terms in the title, abstract, or keywords (see Table S1 in Supplementary Material in the online version at https://doi.org/10.1016/bs.asb.2022.01.002). We excluded articles that were duplicated with previous searches and duplicated between the two databases (Fig. S1 in Supplementary Material in the online version at https://doi.org/10.1016/bs.asb.2022.01.002). Then, we proceeded the same reading steps we previously described for the forward search in *Google Scholar*. All steps of the review included articles from 1987 to January 2020.

Since our aim was to perform a qualitative review, any descriptive information about pre-copulatory and copulatory courtship behaviors in male dimorphic species was included. From the articles selected for our review, we extracted information about the morphology and reproductive tactic of each male morph, type of morph determination (i.e., simple Mendelian inheritance or polyphenism, see Section 4.2), pre-copulatory and copulatory courtship behaviors exhibited by the morphs, and copulation duration for each morph. For the nomenclature used to identify male morphs throughout the text, see Box 1.

BOX 1 Nomenclature of male morphs in terrestrial arthropods.

The terms used to refer to male morphs show great variation in the literature. Taborsky (1997) proposed a unifying nomenclature according to which the term *bourgeois* should be used to refer to males investing in privileged access to mates, including resource or female defense, emission of sexual pheromones, production of nuptial gifts, and/or presence of secondary sexual characters (e.g., weapons and ornaments). In turn, the term *parasitic* should be used to refer to males exploiting the investment of bourgeois conspecifics. These two terms are useful to describe male morphs in several arthropod species included in our review. In harvestmen (*Paecilaemulla lavarrei* and *Serracutisoma proximum*), beetles (*Allomyrina dichotoma*, *Onthophagus* spp., *Prosopocoilus inclinatus*, and *Trachyderes mandibularis*), and damselflies (*Mnais* spp. and *Paraphlebia* spp.), bourgeois males defend territories while parasitic males sneak copulations inside

BOX 1 Nomenclature of male morphs in terrestrial arthropods.—cont'd

these territories or act as satellites (Table 1). Moreover, in some beetles (*Parisoschoenus expositus*), earwigs (*Forficula auricularia*), hemipterans (*Prokelisia dolus*), bees (*Amegilla dawsoni*), and butterflies (*Heliconius charitonia*) bourgeois males guard females while parasitic males search for unmated females (Table 1). In the black field cricket *Teleogryllus oceanicus* and the bladder grasshopper *Bullacris membracioides*, bourgeois males call to attract females while parasitic males act as satellites or search for females, respectively (Table 1). Finally, in *Cardiocondyla* ants, bourgeois males defend females inside the colony while parasitic males mimic the cuticular hydrocarbons of females (Table 1).

However, there are species in our review for which the dichotomy bourgeois-parasitic does not apply. In the harvestman *Equitius doriae* and the firebug *Pyrrhocoris apterus*, the mating tactic of both morphs is based on searching for females (Table 1), and none of them seems to have privileged access to mates. In the spider *Oedothorax gibbosus*, males of the *gibbosus* morph have a gland that produces a nuptial gift while males of the *tuberosus* morph do not have this gland (Table 1). Although males of the *gibbosus* morph can be regarded as bourgeois, males of the *tuberosus* morph cannot be regarded as parasitic because they do not exploit the investment of *gibbosus* males. In fact, in the beginning of the breeding season, only males of the *tuberosus* morph are found in the population (Hendrickx et al., 2015). In the spider *Maevia inclemens*, both the striped and the tufted morph have conspicuous ornaments and perform courtship displays (Table 1), so that no parasitic morph exists. In some cricket species (*Gryllus firmus*, *G. texensis*, *Macroanaxipha macilenta*, and *Velarifictorus ornatus*), morphs differ in wing morphology as well as in calling duration or calling rates (Table 1). However, none of the morphs can be regarded as parasitic because both are able to attract females. The same happens with the firefly *Luciola cerata*, in which the morphs differ in the number and format of the lantern segments (Table 1). Although morphs show differences in the flashing rates, both are able to attract females, and none should be considered parasitic.

Therefore, the dichotomy bourgeois-parasitic does not properly describe the morphs and their reproductive tactics in several species mentioned in our review. To circumvent this problem, we adopted for each species the most frequent terminology used in the literature (e.g., *gibbosus*/*tuberosus*, striped/tufted, long-winged/short-winged, orange-winged/pale-winged, winged/wingless). Moreover, when morph determination is condition dependent (see Section 4.2) and morphs differ mostly in body and weapon size, we use the term *major* for large males with exaggerated weaponry and *minor* for small males with poorly developed or even absent weaponry. In all species included in our review, majors have a reproductive tactic based on female or resource defense, while minors have alternative reproductive tactics that do not involve aggression. For species in which morph determination is based on simple Mendelian inheritance (see Section 4.2) and morphs differ mostly in body and/or ornamentation (e.g., wing coloration), we avoided the dichotomy major-minor.

3. What do we currently know?

3.1 Pre-copulatory courtship

We found information on pre-copulatory and/or copulatory behaviors of male morphs for 33 species of insects and arachnids (Table 1; Fig. 1). In nearly 50% of these studies, there is no reported difference between male morphs for pre-copulatory behaviors (Table 1). This lack of difference should be interpreted with caution because most of the comparisons between male morphs focus only on the *presence/absence* of pre-copulatory courtship (6 studies on 6 species, Table 1) or pre-copulatory courtship *duration* (9 studies on 10 species, Table 1). For only 11 species we have quantitative comparisons between male morphs on other aspects of the pre-copulatory courtship, such as *rates* or *frequencies* of some specific behaviors (earwig: Radesäter & Halldórsdóttir, 1993; beetles: Cook, 1990; Kotiaho, 2002; Okada & Hasegawa, 2005; Simmons & Kotiaho, 2007; Wu et al., 2010; orthopterans: Bertram, 2007; Elias-Quevedo & del Castillo, 2019; spider: Clark, 1994; Table 1). Thus, some subtle qualitative differences or even marked quantitative differences between morphs may exist but have not been noticed. Moreover, the reproductive tactic of the morph in which males fight to monopolize females or resources, exhibit elaborate visual displays, or emit sounds to attract mates is usually more conspicuous to the researchers, and descriptions of pre-copulatory courtship behaviors are focused mostly or exclusively on this morph. It seems that, in many cases, the pre-copulatory courtship behavior of the morph exhibiting more secretive reproductive tactics—which are invariably referred to as "alternatives"—is simply assumed to be similar to the behavior of the other morph.

Qualitative or quantitative differences between morphs in pre-copulatory courtship behaviors were reported for 17 species (Table 1). Among arachnids, there are two spider species in which male morphs show marked morphological differences that are associated with differences in their pre-copulatory courtship behaviors. In the dwarf spider *Oedothorax gibbosus*, males of the *gibbosus* morph have a conspicuous exocrine gland in their cephalothorax that secretes a substance offered to the females as a nuptial gift before copulation. Males of the *tuberosus* morph, in turn, lack this exocrine gland and their pre-copulatory courtship does not involve offering a nuptial gift (Vanacker et al., 2003; Table 1). In the jumping spider *Maevia inclemens*, males of the striped morph have yellow pedipalps, black-and-white striped legs, and gray abdomen with small orange spots (Fig. 1G). They court females at a closer

Table 1 Result of a systematic search on differences between male morphs in pre-copulatory and copulatory courtship.

Taxon	MORPH 1 Morphology	MORPH 1 Mating tactic	MORPH 2 Morphology	MORPH 2 Mating tactic	Differences between male morphs Pre-copulatory courtship	Differences between male morphs Copulation duration	References
ARACHNIDA: Araneae: Linyphiidae							
Oedothorax gibbosus (genetic)	Large exocrine gland on the cephalothorax	Males provide a glandular nuptial gift	No exocrine gland on the cephalothorax	Males do not provide a glandular nuptial gift	Only morph 1 provides nuptial gift	No difference reported for the morphs	Heinemann and Uhl (2000), Vanacker, Maes, Pardo, Hendrickx, and Maelfait (2003), and Maes, Vanacker, Pardo, and Maelfait (2004)
ARACHNIDA: Araneae: Salticidae							
Maevia inclemens (genetic)	Colored body	Males perform a visual display	Black and white body	Males perform a visual display	Morph 2 courts at greater distance	No difference reported for the morphs	Busso and Rabosky (2016), Clark and Biesiadecki (2002)[a], Clark and Morjan (2001), Clark and Uetz (1992, 1993), Clark, Simmons, and Bowker (2018), and **Clark (1994)**[P]
ARACHNIDA: Opiliones: Cosmetidae							
Paecilaemula lavarrei (conditional?)	Larger with large chelicerae	Males fight for territory possession	Smaller with small chelicerae	Males invade territories, and sneak copulations	No difference reported for the morphs	No information available	Solano-Brenes, García-Hernández, and Machado (2018)

Table 1 Result of a systematic search on differences between male morphs in pre-copulatory and copulatory courtship.—cont'd

| Taxon | MORPH 1 | | MORPH 2 | | Differences between male morphs | | References |
	Morphology	Mating tactic	Morphology	Mating tactic	Pre-copulatory courtship	Copulation duration	
ARACHNIDA: Opiliones: Gonyleptidae							
Serracutisoma proximum (conditional?)	Larger with long 2nd pair of legs	Males fight for territory possession	Smaller with short 2nd pair of legs	Males invade territories, and sneak copulations	No difference reported for the morphs	No difference reported for the morphs	Buzatto, Requena, Lourenço, Munguía–Steyer, and Machado (2011) and Buzatto and Machado (2008)
ARACHNIDA: Opiliones: Triaenonychidae							
Equitius doriae (conditional?)	Larger with more robust pedipalps	Males probably search for females	Smaller with less robust pedipalps	Males probably search for females	No difference reported for the morphs	No information available	Hunt (1979)
HEXAPODA: Coleoptera: Cerambycidae							
Trachyderes mandibularis (conditional)	Enlarged mandibles	Males fight for territory possession	Small mandibles	Males search for female	No difference reported for the morphs	No difference reported for the morphs	**Goldsmith** (1985, **1987**)[C] and Goldsmith and Alcock (1993)
HEXAPODA: Coleoptera: Curculionidae							
Parisoschoenus expositus (conditional)	Larger with long horns	Males fight each other for female possession	Smaller with small horns (or hornless)	Males fight for female possession	No difference reported for the morphs	No information available	Eberhard and Garcia-C (2000) and Eberhard, Garcia-C, and Lobo (2000)

HEXAPODA: *Coleoptera: Lampyridae*

Luciola cerata (conditional?)	Flashes with two light segments and the 2nd light segment is pentagonal	Males perform a visual display	Flashes with the first light segment, and the 2nd light segment is semi-oval	Males perform a visual display	Morph 2 has slower flashing rate	No difference reported for the morphs	**Wu, Jeng, South, Ho, and Yang, (2010)[P]**

HEXAPODA: *Coleoptera: Lucanidae*

Prosopocoilus inclinatus (conditional)	Larger	Males fight for territory possession	Smaller	Males fight for territory possession	Morph 2 courts for more time	Morph 2 has longer copulation duration[a]	**Okada and Hasegawa (2005)[P,C]**

HEXAPODA: *Coleoptera: Scarabaeidae*

Allomyrina dichotoma (conditional)	Larger with long horns	Males fight for territory possession	Smaller with short horns (or hornless)	Males search for females	No difference reported for the morphs	Morph 2 has longer copulation duration	Hongo (2003, 2007, 2012), Iguchi (1998, 2010), **Karino and Niiyama (2006)[P,C]**, Karino, Niiyama, and Chiba (2005), and Siva-Jothy (1987)
Onthophagus acuminatus (conditional)	Larger with long horns	Males fight for female possession and invest in parental care	Smaller with short horns (or hornless)	Males search for non-guarded females or sneak copulations, and do not invest in parental care	No difference reported for the morphs	No difference reported for the morphs	Emlen (1997a, 1997b)[a]

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Table 1 Result of a systematic search on differences between male morphs in pre-copulatory and copulatory courtship.—cont'd

| Taxon | MORPH 1 | | MORPH 2 | | Differences between male morphs | | References |
	Morphology	Mating tactic	Morphology	Mating tactic	Pre-copulatory courtship	Copulation duration	
Onthophagus australis (conditional)	Larger with long horns	Males fight for female possession and invest in parental care	Smaller with short horns (or hornless)	Males search for non-guarded females or sneak copulations, and do not invest in parental care	No difference reported for the morphs	No difference reported for the morphs	Kotiaho (2002)[P]
Onthophagus binodis (conditional)	Larger with long horns	Males fight for female possession and invest in parental care	Smaller with short horns (or hornless)	Males search for non-guarded females or sneak copulations, and do not invest in parental care	Morph 2 courts at lower rates	No difference reported for the morphs	Kotiaho (2002)[P], Cook (1990)[P], Tomkins and Simmons (2000)[a], and Simmons and Kotiaho (2007)[P,C]
Onthophagus taurus (conditional)	Larger with long horns	Males fight for female possession and invest in parental care	Smaller with short horns (or hornless)	Males search for non-guarded females or sneak copulations, and do not invest in parental care	No difference reported for the morphs	No difference reported for the morphs	Hunt and Simmons (2002), Knell and Simmons (2010), Kotiaho, Simmons, and Tomkins (2001), Kotiaho, Simmons, Hunt, and Tomkins (2003), Kotiaho (2002)[P], Moczek and Emlen (1999, 2000), and Simmons, Emlen, and Tomkins (2007)

HEXAPODA: Dermaptera: Forficulidae						
Forficula auricularia (conditional)	Larger and with long forceps	Males fight for female possession	Smaller with short forceps	Males sneak copulations	Morph 2 courts for longer time	Morph 2 has shorter copulation duration	**Radesäter and Halldórsdóttir (1993)**[P,C], Tomkins and Brown (2004), **Tomkins and Simmons (1998)**[P], and Walker and Fell (2001)
HEXAPODA: Hemiptera: Delphacidae						
Prokelisia dolus (genetic)	Larger with short wings	Males fight for female possession	Smaller with long wings	Males search for females	No difference reported for the morphs	Morph 2 has longer mating duration	**Langellotto, Denno, and Ott (2000)**[P,C] and Langellotto and Denno (2001)
HEXAPODA: Hemiptera: Pyrrhocoridae						
Pyrrhocoris apterus (genetic)	Long-winged	Males search for females	Short-winged	Males search for females	No difference reported for the morphs	Morph 2 has longer copulation duration	**Socha and Zemek (2004)**[P,C]
HEXAPODA: Hymenoptera: Anthophoridae						
Amegilla dawsoni (conditional)	Larger	Males fight for female possession or wait for females in certain places	Smaller	Males search for unmated females	No difference reported for the morphs	No difference reported for the morphs	Alcock, Simmons, and Beveridge (2005), Alcock (1996a, 1996b, 1996c, 1997a, 1997b), and **Simmons, Tomkins, and Alcock (2000)**[P,C]

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Table 1 Result of a systematic search on differences between male morphs in pre-copulatory and copulatory courtship.—cont'd

Taxon	MORPH 1		MORPH 2		Differences between male morphs		References
	Morphology	Mating tactic	Morphology	Mating tactic	Pre-copulatory courtship	Copulation duration	
HEXAPODA: Hymenoptera: Formicidae							
Cardiocondyla minutior (conditional?)	Wingless	Males fight for female possession inside the nests	Winged	Males search for receptive females outside the nest	Morph 2 courts for less time	Morph 2 has shorter copulation duration	**Mercier et al. (2007)**[P,C] and Yoshizawa, Yamauchi, and Tsuchida (2011)
Cardiocondyla obscurior (conditional?)	Wingless	Males fight for female possession inside the nests	Winged	Males mimic females and search for receptive females outside the nest	No difference reported for the morphs	No difference reported for the morphs	Cremer and Heinze (2003) and Cremer, Schrempf, and Heinze (2011), Du, Schrempf, and Heinze (2007), **Mercier et al. (2007)**[P,C] and Schrempf and Heinze (2008)
Cardiocondyla wroughtoni (conditional?)	Wingless with, more elongate mandibles	Males fight for female possession inside the nests	Winged with less elongate mandibles	Males search for females outside the nest	Morph 2 courts for less time	Morph 2 has longer copulation duration	**Kinomura and Yamauchi (1987)**[P,C]
Hypoponera bondroiti (?)	Larger and wingless	Males fight for female possession	Smaller and winged	Males search for females	No difference reported for the morphs	No difference reported for the morphs	Yamauchi, Kimura, Corbara, Kinomura, and Tsuji (1996)

HEXAPODA: Lepidoptera: Nymphalidae

Heliconius charitonia (genetic)	Larger with long wings	Males fight for female possession	Smaller with short wings	Males search for unmated females	Only morph 2 courts females	No information available	Mendoza-Cuenca and Macías-Ordóñez (2005) and Mendoza-Cuenca and Macías-Odóñez (2010)

HEXAPODA: Odonata: Calopterygidae

Mnais costalis (genetic)	Larger with orange wings	Males fight for territory possession, court and guard females	Smaller with pale wings	Males sneak copulation and do not guard females	Only morph 1 courts females	Morph 2 has longer copulation duration	Hooper, Tsubaki, and Siva-Jothy (1999), Tsubaki, Hooper, and Siva-Jothy (1997), Tsubaki, Samejima, and Siva-jothy (2010), Tsubaki (2003), and **Watanabe and Taguchi (1990)**[C]
Mnais pruinosa (genetic)	Larger with orange wings	Males fight for territory possession, court and guard females	Smaller with pale wings	Males sneak copulation and may guard females	Only morph 1 courts females	Morph 2 has longer copulation duration	**Nomakuchi (1988)**[C], Nomakuchi (1992), and Siva-Jothy and Tsubaki (1989a, 1989b)[a]
Mnais nawai (?)	Larger with orange wings	Males fight for territory possession, court and guard females	Smaller with pale wings	Males sneak copulation and do not guard females	Only morph 1 courts females	No difference reported for the morphs	Nomakuchi and Higashi (1996) and Higashi and Nomakuchi (1997)

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Table 1 Result of a systematic search on differences between male morphs in pre-copulatory and copulatory courtship.—cont'd

| Taxon | MORPH 1 | | MORPH 2 | | Differences between male morphs | | References |
	Morphology	Mating tactic	Morphology	Mating tactic	Pre-copulatory courtship	Copulation duration	
Paraphlebia zoe (?)	Pigmented wing	Males fight for territory possession and guard females	Hyaline wing	Males sneak copulation and do not guard females	No difference reported for the morphs	Morph 2 has longer copulation duration	**Wong–Muñoz, Anderson, Munguía–Steyer, and Córdoba–Aguilar, 2013**[C] and Romo–Beltrán, Macías–Ordóñez, and Córdoba–Aguilar (2009)
Paraphlebia quinta (?)	Pigmented wing	Males fight for territory possession and guard females	Hyaline wing	Males sneak copulation and do not guard females	No difference reported for the morphs	Morph 2 has longer copulation duration	**González–Soriano and Córdoba–Aguilar (2003)**[C]
HEXAPODA: Orthoptera: Gryllidae							
Gryllus firmus (genetic)	Larger with short wings	Males perform an acoustic display	Smaller with long wings	Males perform an acoustic display	Morph 2 has shorter call duration	No information available	Roff and Fairbairn (1993), **Crnokrak and Roff (1995)**[P], and Crnokrak and Roff (1998)
Gryllus texensis (conditional)	Short wings	Males perform an acoustic display	Long wings	Males perform an acoustic display	Morph 2 calls more than morph 1	No information available	**Bertram (2007)**[P] and Guerra and Pollack (2007, 2010)

Teleogryllus oceanicus (genetic)	Normal wing morphology	Males perform an acoustic display	Flat wing (unable to call)	Males act as satellites	Only morph 1 calls	No difference reported for the morphs	Zuk, Rotenberry, and Tinghitella (2006), Zuk, Bailey, Gray, and Rotenberry (2018), Tinghitella (2008), Tinghitella, Wang, and Zuk (2009), and Rayner, Aldridge, Montealegre, and Bailey (2019)
Velarifictorus ornatus (conditional?)	Short wings	Males perform an acoustic display	Long wings	Males perform an acoustic display	No difference reported for the morphs	No information available	Zhao, Lin, and Zhu (2017)
Macroanaxipha macilenta (?)	Wider forewings	Males perform an acoustic display	Narrow forewing	Males perform an acoustic display	Morph 2 produces shorter and lower calls	Morph 2 has longer copulation duration and transfer two spermatophores	**Elias–Quevedo and del Castillo (2019)**[C]
HEXAPODA: Orthoptera: Pneumoridae							
Bullacris membracioides (conditional)	Larger and winged	Males perform an acoustic display	Smaller and wingless (unable to call)	Males search for females	Only morph 1 calls	No information available	Donelson and Van Staaden (2005) and Van Staaden & Römer (1997)

[a]We are considering the mounting time, which is a behavior that precedes copulation and cannot be regarded as copulation per se.

The list includes only species in which differences between morphs in pre-copulatory and/or copulatory courtship are explicitly mentioned in the paper. Studies that provide quantitative comparisons between morphs on their pre-copulatory courtship behavior (P) and/or copulation duration (C) are indicated in bold.

distance and crouch down while moving back and forth. Males of the tufted morph are characterized by three tufts of hair on the anterior margins of the cephalothorax, black body, and white legs (Fig. 1H). They court females from afar and stand on the tip of their legs while waving their abdomen from side to side (Clark, 1994; Table 1).

In some insect species, differences between morphs in pre-copulatory courtship behaviors are also mainly related to morphology. In the black field cricket *Teleogryllus oceanicus* and the bladder grasshopper *Bullacris membracioides* (Fig. 1F), males of one morph (flatwing and wingless, respectively) are unable to call and thus their pre-copulatory courtship lacks the acoustic component (Donelson & Van Staaden, 2005; Zuk et al., 2006; Table 1). In three cricket species (*Gryllus firmus*, *G. texensis*, and *Macroanaxipha macilenta*), male morphs differ in wing morphology, with one morph exhibiting longer or wider wings than the other morph (Table 1). This difference in wing morphology is coupled with differences in calling duration or calling rates (Table 1). In a similar way, in the firefly *Luciola cerata*, male morphs differ in the morphology and number of lantern segments, where are located the bioluminescent organs. Whereas one morph has large body size and two lantern segments, with the second one showing pentagonal shape, the other morph has small body size and only one lantern segment with semi-oval shape. This morphological difference is coupled with a difference in the flashing rates, so that males with two lantern segments have a faster flashing rate than those with only one lantern segment (Wu et al., 2010; Table 1).

In two species of beetles (*Prosopocoilus inclinatus* and *Onthophagus binodis*), one species of earwig (*Forficula auricularia*), and two species of ants (*Cardiocondyla minutior* and *C. wroughtoni*), male morphs differ in the total duration or the rate of pre-copulatory courtship, which usually comprises tactile stimulation performed with different body parts (Table 1). Among beetles and earwigs (Fig. 1C–E), particularly, there is one morph in which males are larger and have well developed weapons, and another morph in which males are smaller and have poorly developed weapons or no weapon at all (beetles: Cook, 1987; Goldsmith, 1985; Okada & Hasegawa, 2005; earwigs: Radesäter & Halldórsdóttir, 1993; Table 1). Despite this marked morphological difference between morphs, there is not a general pattern about behavioral differences between morphs in their pre-copulatory courtship. Depending on the species, either the large or the smaller morph can show more intense or longer courtship behaviors (Table 1).

Finally, in four insect species, males of one morph exhibit pre-copulatory courtship, whereas males of the other morph simply do not court the females. In the butterfly *Heliconius charitonia*, males of the morph with larger

and longer wings mate with females as soon as they emerge from the pupal case and show no courtship behavior. In turn, males of the morph with smaller and shorter wings do not guard pupal cases, but rather actively search for unmated females and court them before copulation (Mendoza–Cuenca & Macías-Odóñez, 2010; Table 1). In the damselflies *Mnais costalis, M. nawai*, and *M. pruinosa* larger males with orange wings (Fig. 1A) defend territories containing oviposition sites and court visiting females hovering in front of them. Smaller males with pale wings (Fig. 1B) do not defend territories and never court females (Higashi & Nomakuchi, 1997; Nomakuchi, 1992; Watanabe & Taguchi, 1990; Table 1).

3.2 Copulatory courtship

We found no study that provides data on the behavior of each male morph during copulation. The only information available in the studies was related to *copulation duration*, which was reported for 25 species (Table 1). In most species ($n = 14$), no difference between morphs in copulation duration was reported (Table 1). In 11 species, copulation duration was reported to be different between morphs, and in 9 of these species males of the morph exhibiting ARTs (i.e., satellites, sneakers, or female mimics) copulate for longer time (Table 1). We stress, however, that only 16 studies on 15 species provided formal statistical comparisons between morphs about copulation duration (Table 1).

4. Processes underlying differences between male morphs in pre-copulatory courtship

There are several processes that may promote differences in pre-copulatory courtship between male morphs. In what follows, we classify these processes into four main groups based on the empirical examples we found in our review (Table 1): (1) traits used in pre-copulatory courtship may be present in only one of the male morphs, thus leading to marked qualitative differences in their pre-copulatory behaviors; (2) only males of the morph in good condition may be able to pay the costs of energetically demanding courtship behaviors; (3) female resistance to the courtship of one morph may induce longer or more elaborated courtship behaviors by males of this morph as a way of increasing their chances of being accepted as mates; and (4) when male–male agonistic interactions are intense, males of the smaller or less aggressive morph should abbreviate the courtship behavior to avoid interference or injuries imposed by males of the larger and more aggressive morph.

4.1 Male dimorphism in traits used for pre-copulatory courtship

Although females accept mating with both male morphs in many male-dimorphic species of insects (e.g., Alcock, 1996a; Briceño & Eberhard, 1995; Cook, 1990; Kotiaho, 2002; Okada & Hasegawa, 2005; Radesäter & Halldórsdóttir, 1993; Walker & Fell, 2001; Wong-Muñoz et al., 2013; Wu et al., 2010) and arachnids (e.g., Buzatto et al., 2011; Clark & Uetz, 1992; Radwan, 1997; Solano-Brenes et al., 2018; Vanacker et al., 2003), it does not mean that they show no preference for one morph over the other. There are some species in which females show clear pre- and post-copulatory preferences for one of the morphs, usually the one bearing a morphological trait used in pre-copulatory courtship. In the spider *Oedothorax gibbosus*, for instance, mating experiments showed that *gibbosus* males, which bear the nuptial gift gland, are more readily accepted by, and sire more offspring of already fertilized females when compared with *tuberosus* males, which lack the nuptial gift gland (Hendrickx, Vanthournout, & Taborsky, 2015; Vanacker, Hendrickx, Maes, Verraes, & Maelfait, 2004). These findings suggest that *gibbosus* males are more attractive to females, probably because their pre-copulatory courtship involves offering a potently nutritious gift that may provide direct benefits to the females (Hendrickx et al., 2015; Vanacker et al., 2004, 2003). Despite their lower attractiveness, *tuberosus* males obtain most fertilizations early in the breeding season because *gibbosus* males take longer to reach adulthood. The asynchrony in the phenology of the two male morphs may explain the maintenance of male dimorphism associated with two forms of pre-copulatory courtship, one with high male investment in nuptial gift and another with no investment in nuptial gift (Hendrickx et al., 2015).

There are other male-dimorphic species in which only one morph has the traits used in pre-copulatory courtship, such as stridulatory organs (e.g., Clark & Morjan, 2001; Donelson & Van Staaden, 2005; Zuk et al., 2006). This is the case of some cricket and grasshopper species in which some males have well-developed wings and are able to produce sounds that attract females (Fig. 1F). Males with modified or even absent wings are unable to produce sounds and their reproductive tactic is based on satelliting calling males or actively searching for females (Table 1). In the black field cricket *Teleogryllus oceanicus*, females prefer calling males even in islands where the entire male population is composed of the flat wing morph, which is unable to produce sounds (Tinghitella & Zuk, 2009). However, male

dimorphism is maintained in mixed–morph populations probably because a small fraction of females from all populations occasionally accept mating with flat wing males (Tinghitella & Zuk, 2009).

In conclusion, pre-copulatory courtship can differ between male morphs simply because a conspicuous trait used for attracting and enticing the female to mate is present in only one morph. Although females usually show sexual preference for males bearing the sexually selected trait involved in pre-copulatory courtship, males not bearing this trait can be maintained in the populations because at least some females accept mating with them.

4.2 Costs of pre-copulatory courtship behaviors

In terrestrial arthropods, male morphs are determined by one of two mechanisms: (i) simple Mendelian inheritance involving one or a few alleles or (ii) condition dependence, a type of phenotypic plasticity known as polyphenism in which environmental conditions play a predominant role in morph determination (reviewed in Buzatto et al., 2014, Emlen, 2008, and Radwan, 2009). The cues that trigger the expression of condition dependent male dimorphism include, for instance, temperature, photoperiod, and population density, but the most intensively studied is body condition (examples in Buzatto et al., 2014, Emlen, 2008, and Tomkins & Hazel, 2007). Although "body condition" is an elusive term, we adopt the following operational definition: it is the amount of resources acquired by an individual and the efficiency with which these resources are allocated to morphological, behavioral, or physiological traits (modified from Bussière, Hunt, Stölting, Jennions, & Brooks, 2008 and Rowe & Houle, 1996). How to measure body condition is a long–lasting problem, which has already been addressed in previous papers (reviewed in Stahlschmidt & Chang, 2021). For the purposes of our arguments, it is enough to know that there is strong evidence for insects and arachnids showing that the expression of ornaments and weapons is condition dependent, which means that the size of these traits covary positively with food acquisition during immature stages (e.g., Bonduriansky, 2007; Cotton, Fowler, & Pomiankowski, 2004; Emlen, Warren, Johns, Dworkin, & Lavine, 2012; Taylor, Clark, & McGraw, 2011).

Among polyphenic arthropods, males that experience low food availability or quality during immature stages (i.e., poor condition males) tend to become *minors*, which are adults with small body size and poorly developed secondary sexual traits (Box 1). In turn, males that experience high food

availability or quality during immature stages (i.e., good condition males) tend to become *majors*, which are males with large body size and exaggerated secondary sexual traits (Box 1). Therefore, every male in the population can express either the major or the minor morph, and the quantity or quality of food acquired by each individual during development is the main determinant of its phenotype as adult (Buzatto et al., 2014; Gross, 1996; Tomkins & Hazel, 2007; West-Eberhard, 2003). If a male achieves a certain value of body mass during development (i.e., a size threshold), he may derive more fitness benefits by continuing to grow to become a major, whose reproductive tactic is based on fighting for females or resources. If the size threshold is not achieved, a male may derive more fitness becoming a minor that exhibits reproductive tactics not involving aggression (Brockmann, 2008; Buzatto et al., 2014; Eberhard, 1982). To which extent the quantity or quality of food acquired during development also affects the energy reserves of adult males is an open question in terrestrial arthropods. In recent years, however, there is growing evidence of the so-called carryover effects, which occur when the previous experience of an individual explains its current performance in a given task (see review in O'Connor, Norris, Crossin, & Cooke, 2014). If males that experienced low food availability or quality during immature stages become poor condition adults, they may have low energy reserves to perform costly behaviors, which may compromise their reproductive performance.

Pre-copulatory courtship in insects and arachnids includes a wide range of visual, acoustic, tactile, seismic, and chemical displays, usually performed by males with the main function of convincing females to accept mating. Females select their potential mating partners based (at least in part) on these displays, which are therefore under intersexual selection (examples in Choe & Crespi, 1997 and Thornhill & Alcock, 1983). Given the costs of several pre-copulatory courtship behaviors, only good condition males are able to express high intensity displays (reviewed in Byers, Hebets, & Podos, 2010 and Clark, 2012; see also Olivero, Vrech, Oviedo-Diego, Mattoni, & Peretti, 2019 and references therein). In some species, poor condition males may even rely on non-courting reproductive tactics to have access to females. In the grasshopper *Melanoplus sanguinipes*, for instance, there are two reproductive tactics, although males are not dimorphic. Well-fed males court females by vibrating their femora in front of them. If the female is receptive and displays in response, the male leaps on her and copulation takes place. Poorly fed males do not court females; instead, they stalk females and leap on them from behind. Most females react to the

approach of these males by jumping away or kicking them off with their hind legs. Only a small fraction of these apparently coercive mating attempts results in copulations (see Belovsky, Slade, & Chase, 1996 and references therein).

Among polyphenic arthropod species, we could not find any unequivocal example of coercive mating attempts by minors (Table 1), but body condition is known to affect the *intensity* of pre-copulatory courtship behaviors in some species. In the firefly *Luciola cerata*, for instance, the pre-copulatory flashing display is very costly (Goh & Li, 2011) and males of the smaller morph with only one lantern segment flash at slower rates than males of the larger morph with two lantern segments (Wu et al., 2010; Table 1). It is not yet known if morph determination is condition dependent in this species, i.e., whether body size and the number of lantern segments are determined by the amount of food to which males had access during the larval stage. However, given that adult males do not feed (Wu et al., 2010), the energy reserves allocated to the costly pre-copulatory display are likely dependent on larval nutrition (i.e., the quantity and/or quality of the food they acquired). Thus, large males with faster flashing rates probably experienced higher food availability during development than small males with slower flashing rates. This is a putative example of carryover effect in male-dimorphic arthropods because the courtship performance of adult males is likely explained by their previous nutritional experience during the larval period.

A different example of how body condition may affect the intensity of pre-copulatory courtship behaviors in male-dimorphic arthropods comes from dung beetles of the genus *Onthophagus*. In these well-studied beetles, males court females by tapping their dorsum with the head and forelegs in bouts that last a few seconds (Cook, 1990). A laboratory experiment showed that adult males of three species (*O. australis*, *O. binodis*, and *O. taurus*) manipulated to have abundant food resources (good condition males) had higher courtship rates than males manipulated to have limited food resources (poor condition males). Moreover, courtship rates had a marked positive effect on male mating success in the three species (Kotiaho, 2002). Taken together, these findings indicate that adult males that have access to more food can increase their body condition and consequently their courtship rates. Under natural conditions, fresh dung patches are usually monopolized by majors, which are large and bear long horns (Emlen, 1997a; see also Fig. 1E). Therefore, on average, majors should have access to more food than minors and exhibit a higher intensity of pre-copulatory courtship behaviors.

In conclusion, some pre-copulatory courtship behaviors are condition dependent, so that only well-fed males have energy to exhibit high intensity behaviors. Poorly fed males, in turn, are expected to exhibit low intensity behaviors, which could render them less attractive to the females. In fact, for both the firefly *L. cerata* (Wu et al., 2010) and the *Onthophagus* dung beetles (Kotiaho, 2002), females prefer males that exhibit high intensity pre-copulatory courtship behaviors. Thus, studies with these insects suggest that females use the intensity of costly pre-copulatory courtship behaviors to evaluate potential mates, and that good condition males should have, on average, higher mating success than poor condition males.

4.3 Female resistance

In species in which males monopolize resources, such as oviposition sites or food patches, vagrant females should approach the best territories (i.e., those containing high-quality resources) and mate with their owners. If high-quality territories are scarce, male-male competition for territory possession is expected to be intense, so that only the largest or strongest males will accumulate as territory owners (see discussion in Thornhill & Alcock, 1983). Because the possession of high-quality territories may indicate male quality (e.g., size, strength, fighting ability), female mating decisions can be determined mainly by territory quality, rather than male traits, such as pre-copulatory courtship behaviors (i.e., "indirect mate choice" sensu Wiley & Poston, 1996). In extreme cases, territory owners could not even court females that visit their territories. Assuming that non-territorial males are smaller, weaker, and probably less attractive to females, they are expected to face some female resistance when trying to sneak copulation inside or outside a territory. Therefore, non-territorial males could increase their chances of being accepted as mates by performing more intense or more elaborate pre-copulatory courtship, which ultimately would promote quantitative or even qualitative differences between male morphs in their courtship behaviors. This hypothesis implies (i) the presence of pre-copulatory courtship behaviors in the species, (ii) female polyandry, and (iii) female plasticity in their mating preferences according to male morph.

The scenario described above has not been reported for any species included in Table 1, but there is one butterfly species in which a similar form of indirect mate choice may explain extreme differences between morphs in their pre-copulatory courtship. In several butterflies of the genus *Heliconius*, including *H. charitonia*, some males perform pupal mating

(Mendoza–Cuenca & Macías-Odóñez, 2010; Table 1). In this mating system, males molt to adulthood before females and search for female pupae on the vicinity of host plants (Brown, 1981). Males compete with each other for perching on female pupae and for accessing the emerging female (e.g., Deinert, Longino, & Gilbert, 1994; Hernández & Benson, 1998). Male-male competition during their tenure on a female pupa may be so intense that some males are frequently found lying exhausted or dead on the ground. Pupal mating is an example of indirect mate choice because females do not have to respond to differences in male size, yet perching males are larger than males that fail to perch on a female pupa (Deinert et al., 1994; Mendoza-Cuenca & Macías-Odóñez, 2010). Thus, although females are unable to resist mating attempts immediately after emergence, they may still copulate with the best mates because male size influences the outcome of male-male competition for the pupae. However, some female pupae of *H. charitonia* are not detected by males, so that females do not mate immediately after emergence. While foraging, these females are found by small males, which do not perform pupal mating. Contrary to large males, small males perform pre-copulatory courtship and females may resist to their mating attempts by flying away (Mendoza–Cuenca & Macías-Odóñez, 2010). Although pupal mating may be regarded as a kind of forced copulation (Markow, 2000), female resistance is still a valid explanation for the extreme differences between male morphs in their pre-copulatory courtship. While large males achieve copulation without courting emerging females (since they are unable to resist), small males cannot force copulation and need to court vagrant females.

It is possible that quantitative (rather than qualitative) differences between morphs in pre-copulatory courtship caused by female resistance occur in at least two species that appear in our review: the stag beetle *Prosopocoilus inclinatus* and the earwig *F. auricularia* (Table 1). Females of the stag beetle are initially resistant to courting males often kicking the potential mate or moving away from him (Okada & Hasegawa, 2005). Although females resist copulation attempts of both morphs, they accept copulation more rapidly with larger males bearing longer mandibles. Smaller males bearing shorter mandibles persist more in courtship behaviors to achieve copulation, leading to longer pre-copulatory interactions (Okada & Hasegawa, 2005). Females of the earwig *F. auricularia* have a similar behavior, initially resisting copulation attempts of both male morphs (Radesäter & Halldórsdóttir, 1993). However, larger males bearing longer forceps are accepted faster than small males bearing shorter forceps

(Radesäter & Halldórsdóttir, 1993). Morover, when large males had their forceps experimentally shortened, females also take longer to accept copulation with them (Tomkins & Simmons, 1998). Taken together, these findings suggest that females of at least some species evaluate male-dimorphic traits during pre-copulatory courtship to make their mating decisions. They also suggest that males' pre-copulatory behavior is highly flexible and that minors can adjust the duration and perhaps the intensity of this behavior in response to female resistance, as have already been reported for non-dimorphic males of some scorpion species (e.g., Peretti & Carrera, 2005).

It is important to stress that females of some terrestrial arthropods with male dimorphism apparently do not resist to the mating attempts of non-territorial males. This is the case of the harvestman *Serracutisoma proximum* (Buzatto et al., 2011) and damselflies of the genus *Mnais* (Higashi & Nomakuchi, 1997; Nomakuchi, 1992; Nomakuchi, Higashi, Harada, & Maeda, 1984; Tsubaki et al., 1997; Watanabe & Taguchi, 1990). In the damselflies, large and orange-winged males (Fig. 1A) defend territories containing suitable oviposition sites, i.e., submerged rotting wood. Females visit these territories and are courted by the males, which hover in front of them (Table 1). In *M. costalis*, only 39% of the visiting females copulate with the territory owner (Watanabe & Taguchi, 1990), indicating that females evaluate male and/or territory traits to make their mating decisions. Territorial males that achieve copulation usually guard the mating partner during oviposition, preventing the approach of other males. Small males and pale-winged males (Fig. 1B) do not defend territories and do not exhibit any pre-copulatory courtship (Table 1). Despite the lack of a territory and pre-copulatory courtship displays, nearly 66% of the mating attempts of pale-winged males lead to copulation (Watanabe & Taguchi, 1990).

There are many possible reasons why females accept copulation with a non-territorial male, even when they have already copulated with a territorial male. These reasons include, for instance, reduced risk of sperm limitation, reduced risk of genetic incompatibility with the territorial male, and increased genetic variability of the offspring (reviewed in Arnqvist & Nilsson, 2000 and Reichard, Le Comber, & Smith, 2007). Thus, whenever females derive benefits from polyandry, they should also accept sneak copulations by other males that are successful in evading the surveillance of territorial males. In these cases, we should expect no remarkable difference between morphs in the duration and/or intensity of pre-copulatory

courtship behaviors. An alternative explanation is that females accept sneak copulations simply to avoid the waste of time and energy needed to reject males (i.e., "convenience polyandry," Boulton, Zuk, & Shuker, 2018). This explanation assumes that females have full control of the fate of the sperm they receive, which seems to be the case in several species of insects and arachnids (Eberhard, 1996, 2015; Macías-Ordóñez, Machado, Pérez-González, & Shultz, 2010). In *Mnais* damselflies, for instance, immediate remating with a territorial male, which can displace the sperm of non-territorial males, gives the female the possibility to control the paternity of her offspring (see Sections 5.1 and 5.2).

4.4 Male-male agonistic interactions

In many species of insects and arachnids, the reproductive tactic exhibited by males of the larger or more aggressive morph is based on agonistic interactions for the monopolization of females or resources used by females, such as oviposition sites (examples in Brockmann, 2008 and Buzatto & Machado, 2014). In turn, the reproductive tactic exhibited by males of the smaller or less aggressive morph almost never involves agonistic interactions (examples in Brockmann, 2008 and Buzatto & Machado, 2014). Instead, these males usually rely on ARTs, such as active search for females outside the territories defended by large males (e.g., *Trachyderes mandibularis*; Goldsmith & Alcock, 1993), invasion of territories to sneak copulations with the females inside the territories (e.g., *Serracutisoma proximum*; Buzatto et al., 2011), interception of females in the vicinities of the territories (e.g., *Mnais* spp.; Nomakuchi & Higashi, 1996), or even female mimicking (e.g., *Cardiocondyla* spp.; Mercier et al., 2007). All these reproductive tactics require that males of the smaller or less aggressive morph come close to males of the larger and more aggressive morph, thus facing the risk of being detected, attacked, and even injured. If the risk of being detected is high and the detection leads to male-male agonistic interactions, or if the risk of being detected is low, but the injury risk in male-male agonistic interactions is high, males exhibiting ARTs should abbreviate the pre-copulatory courtship. By doing so, these males can mate fast, reducing the risk of interference and/or injuries imposed by males of the larger and more aggressive morph.

We visualize at least four non-exclusive situations in which males of the smaller or less aggressive morph have high chance of being detected and injured by males of the larger and more aggressive morph: (i) when they

need to invade a territory or harem to have access to the females (e.g., Munguía-Steyer, Buzatto, & Machado, 2012), (ii) when territory or harem size is small, so that the owner male can easily guard all females (e.g., Munguía-Steyer et al., 2012), (iii) when females are confined to places, such as nests or cavities in fallen logs, that can be easily monitored by the owner male (e.g., Kelly, 2004; Kinomura & Yamauchi, 1987); and (iv) when pre-copulatory displays are conspicuous (e.g., visual or acoustic) and attract the attention of other males nearby (e.g., Zeng, Zhu, & Kang, 2016). Our hypothesis that males of the smaller or less aggressive morph modulate their pre-copulatory behavior in response to the risk of being detected and attacked by males of larger and more aggressive morph assumes that females accept copulations with other males that are successful in evading the sur-veillance of territorial males, even if the invaders show low rates of pre-copulatory courtship. As we have seen in Sections 4.1 and 4.3, this assumption is reasonable because females of several male-dimorphic species are highly polyandrous.

Agonistic interactions between males may explain the differences in pre-copulatory courtship reported for male morphs of two ant species belonging to the genus *Cardiocondyla* (Table 1). In this genus, males of the wingless morph stay in the natal nest and fight each other for the pos-session of females. Contrary to what happens with beetles, damselflies, and earwigs, male–male agonistic interactions in *Cardiocondyla* are potentially lethal, and therefore highly risky for the males (Stuart, Francoeur, & Loiselle, 1987). Males of the winged morph do not fight and can live unnoticed inside the natal nest because their cuticular hydrocarbon profile is similar to that of the females. Thus, they chemically mimic females and can copulate with them on their natal nest without being noticed by aggressive wingless males (Cremer, Sledge, & Heinze, 2002). However, the chemical mimicry of older winged males is less effective, and they are often detected by resident wingless males (Cremer et al., 2008). In this scenario, older winged males are expected to reduce their pre-copulatory courtship duration to decrease their chances of being detected and injured by aggressive wingless males. In fact, when wingless males are present in the colony, winged males disperse to other colonies sooner than when wingless males are absent (Cremer et al., 2011). An experimental manipulation of colonies with and without chem-ical cues of wingless males could be used to investigate whether older winged males plastically adjust the duration of their highly elaborate pre-copulatory courtship display (see Mercier et al., 2007) in response to the risk of injuries.

Another species in which male–male agonistic interactions may lead to differences between male morphs in their pre-copulatory courtship is the horned beetle *Allomyrina dichotoma*. Whereas long-horned males engage in contests for the possession of areas on oak trees that exude sap, short-horned males avoid agonistic interactions (Iguchi, 2010; Siva–Jothy, 1987). Contests between long-horned males can result in serious damages, such as loss of the horn or ripping the elytra and wings (Siva–Jothy, 1987). Short-horned males avoid these contests starting to seek females early in the night, when long-horned males are not active yet (Siva–Jothy, 1987). Because the risk of being detected and injured in the early hours of the night is low, short-horned males are able to spend more time than long-horned males accomplishing pre-copulatory courtship (Karino & Niiyama, 2006). This long courtship may increase the chance of a supposedly less attractive male morph being accepted by the females and explain why the proportion of copulations in nature is similar for males of both morphs (Siva–Jothy, 1987).

A final example of a male-dimorphic species in which male-male agonistic interactions may lead to differences between morphs in pre-copulatory courtship duration is the harvestman *Paecilaemula lavarrei*. Large males bear powerful chelicerae (Fig. 1) and fight each other for the possession of territories on tree trunks and fallen logs. The agonistic interactions between males may result in severe injuries, such as leg amputation caused by the rival (Solano-Brenes et al., 2018). Given that males of both morphs use their legs for locomotion and chemo- and mechano-reception (Shultz & Pinto–da–Rocha, 2007; Willemart, Farine, & Gnaspini, 2009), amputations during contests may represent high costs to the males. Moreover, the first two pairs of legs are also used by both morphs in pre-copulatory courtship (Solano-Brenes et al., 2018), then agonistic interactions that lead to leg amputation can impose additional costs in terms of future reproduction. Therefore, small males of *P. lavarrei*, which bear delicate chelicerae (Fig. 1J) and do not defend territories, should engage in pre-copulatory courtship for shorter time than majors, minimizing the chances of being detected and injured by a territory owner. Although Solano-Brenes et al. (2018) do not report qualitative differences in pre-copulatory courtship of the morphs, they did not perform a quantitative comparison of courtship duration. Because this species can be maintained in the laboratory, where fights and copulations are easily observed, the species is a suitable study system to explore the role of male-male agonistic interactions on the duration of pre-copulatory behaviors exhibited by males of the smaller and less aggressive morph.

As final remark, we stress that physical injuries are not the rule in male–male agonistic interactions of male-dimorphic arthropods. In many

species, fights for the possession of females or resources lead to no physical injury (damselflies: e.g., Higashi, 1981; Watanabe & Taguchi, 1990; dung beetles: e.g., Eberhard, 1980; Emlen, 1997a; bees: e.g., Alcock, 1996a). However, even in these species, males of the larger or more aggressive morph may disrupt the pre-copulatory courtship of males of the smaller or less aggressive morph. In our review on male-dimorphic arthropods, we could not find any description of male attempts to interrupt the pre-copulatory courtship of rivals. As we are going to discuss in Section 5.1, all available reports refer to male–male agonistic interactions during and after copulation (e.g., Eberhard & Garcia-C, 2000; Walker & Fell, 2001). Despite the lack of behavioral reports of male–male agonistic interactions before copulation, it is reasonable to predict that males of the smaller or less aggressive morph would abbreviate the pre-copulatory courtship if the risk of interruption by males of the larger or more aggressive morph is high.

5. Differences between morphs in copulatory courtship: What can we expect?

Since Parker (1970) proposed the concept of sperm competition, we know that sexual selection continues to act during and after copulation (reviewed in Birkhead, 2014). Parker (1990) himself developed a sperm competition model for species exhibiting ARTs. The model assumes that sperm competition obeys a "raffle principle," which means that the fertilization probability increases with the proportion of sperm of a given male inside the female reproductive tract. The model also assumes that males of the fighter morph are paired permanently to particular females (i.e., a harem-like mating system), while males of the non-fighter morph sneak copulations with already mated females. The results of this game-theoretical model predict lower expenditure on ejaculate production by males of the fighter morph because the probability of sperm competition for them is lower than for the non-fighter morph. However, the magnitude of the difference between morphs decreases as the frequency of the non-fighter morph increases in the population (reviewed in Parker & Pizzari, 2010 and Simmons, Lüpold, & Fitzpatrick, 2017). In some terrestrial arthropods, the gonadal investment and/or ejaculate volume of minors (i.e., the non-fighter morph) are indeed higher than majors (i.e., the fighter morph) (e.g., Kelly, 2008; Reynolds & Byrne, 2013; Schrempf, Moser, Delabie, & Heinze, 2016; Simmons, Parker, & Stockley, 1999; Tomkins & Simmons, 2002;

but see Munguía-Steyer et al., 2012 and Simmons et al., 1999). Thus, sperm competition seems to differ between majors and minors, leading to different selective pressures on males of each morph during the post-copulatory phase (see discussion in Kustra & Alonzo, 2020 and Simmons, 2001).

Although important, sperm competition is only one of the post-copulatory processes that may affect the fertilization success of the males. Cryptic female choice is another important post-copulatory process in species with internal fertilization, such as all terrestrial arthropods (Eberhard, 1991, 1996; Peretti & Aisenberg, 2015). According to Eberhard (2015), cryptic female choice "includes paternity biases which result from differences in the expression of female activities that come into play during and following copulation with different males and that favor males with particular traits over others which lack these traits." Cryptic female choice is known to be a powerful process leading to diversification of male genitalia in terrestrial arthropods (reviewed in Eberhard, 2010a, 2010b, Hosken & Stockley, 2004 and Simmons, 2014). However, the relevance of cryptic female choice in shaping possible differences in the copulatory behavior of each male morph is still poorly understood. Moreover, the role of post-copulatory processes on genital differentiation between male morphs is a largely unexplored subject in arthropods (but see House & Simmons, 2007; see also Gilman, Corl, Sinervo, & Irschick, 2019 for an example in a male-polymorphic lizard).

There are some studies showing that male genitalia show great within and between population variation in insects and arachnids, but none of these species exhibits male dimorphism (e.g., butterflies: Gilligan & Wenzel, 2008; Goulson, 1993; odonates: Córdoba-Aguilar & Cordero-Rivera, 2008; spiders: Jocqué, 2002; Lai, Maddison, Ma, & Zhang, 2021). In butterflies, there are also some reports of within species variation in male genitalia in species exhibiting discrete polymorphism. In these species, however, both males and females are dimorphic, which suggests that factors other than sexual selection (e.g., climatic seasonality) are driving morph determination and genitalic differentiation (e.g., Fumi & Friberg, 2019; Mutanen & Kaitala, 2006). Finally, there are some interesting cases of species in which males show marked genital dimorphism. This is the case of some species of praying mantis of the genus *Ciulfina*, for which there is dimorphism in the orientation of male genitalia. Within the same population, there are males with right-oriented and left-oriented genitalia (Holwell & Herberstein, 2010). Another example comes from the male-dimorphic thrips *Iotatubothrips kranzae,* in which the male genitalia are about 55% longer in the long-winged morph than in the short-winged morph (Mound, Crespi, & Tucker, 1998).

Although there is evidence showing that male genital dimorphism is not driven by reproductive isolation (Holwell & Herberstein, 2010), the mechanisms leading to the evolution this dimorphism in both praying mantis and thrips are not yet understood.

In the next two sections, we first explore scenarios in which the copulatory behavior of male morphs may differ in response to different selective pressures acting on each of them. Then, we discuss the possibility of disruptive sexual selection on the morphs leading to within species variation in their genital morphology.

5.1 Copulatory behavior and female stimulation

In the previous section, we showed that females may have mating preferences for males bearing exaggerated sexually selected traits, such as ornaments, weapons, and glands that produce nuptial gifts, or for males exhibiting high intensity pre-copulatory courtship behaviors. Female preference for these males may extend to the copulatory and post-copulatory phase. In this scenario, males bearing reduced sexually selected traits could perform more intense or more elaborate copulatory courtship and female genital stimulation. By doing so, non-preferred males could circumvent possible disadvantages in sperm competition and overcome female-imposed barriers to gain access to their gametes. Given that copulatory courtship in terrestrial arthropods involves mainly tactile stimulation with non-intromittent (e.g., legs, antennae, forceps) and intromittent (i.e., genitalia) structures (examples in Peretti & Aisenberg, 2015), we argue that it has lower costs than conspicuous pre-copulatory courtship displays, such as sound production (e.g., Hunt et al., 2004), long-lasting repetitive movements (e.g., Kotiaho et al., 1998), or production and offering of nuptial gifts (e.g., Macedo-Rego, Costa-Schmidt, Santos, & Machado, 2016). Thus, even when males experience a poor diet during development or are poorly fed as adults (poor condition males), they could be able to perform high intensity or long-lasting genital stimulation. However, we stress that quantifications of the costs paid by males to perform copulatory courtship behaviors are extremely rare in the literature (e.g., Cargnelutti et al., 2021; Watson & Lighton, 1994).

A long-lasting female genital stimulation could explain why copulation duration of two beetle species, namely, *Allomyrina dichotoma* and *Prosopocoilus inclinatus*, is longer for minors, which could be regarded as non-preferred mating partners when compared with majors (Karino & Niiyama, 2006;

Okada & Hasegawa, 2005; Table 1). In the earwig *Forficula auricularia*, however, copulation duration is longer for majors than for minors (Table 1), but this pattern was observed only when the sex-ratio was experimentally manipulated to be male-biased (Radesäter & Halldórsdóttir, 1993). Frequent interference of majors over minors during mating interactions may explain why copulation duration is shorter in the latter. In fact, Radesäter and Halldórsdóttir (1993) report that majors are more successful than minors in separating a pair in copula, which clearly abbreviates copulation duration of minors. Agonistic interactions between morphs may also explain why copulation duration of winged males of at least one species of *Cardiocondyla* ants is shorter than that reported for aggressive wingless males (Mercier et al., 2007; Table 1). Here, it is important to stress that, without any external interference, copulation duration may be under either male or female control, depending on the sex that initiates and terminates copulation (Eberhard, 1996). Unfortunately, we do not know if it is the case for most of the male-dimorphic species mentioned here, and thus any link between copulation duration and post-copulatory processes should be made with caution.

In damselflies of the genera *Mnais* and *Paraphlebia* (Table 1), satellite males do not show any pre-copulatory courtship behavior (González-Soriano & Córdoba-Aguilar, 2003; Watanabe & Taguchi, 1990) but their copulation duration is longer than that of territorial males (Siva-Jothy & Tsubaki, 1989a; Wong-Muñoz et al., 2013; González-Soriano & Córdoba-Aguilar, 2003; Table 1). Following the same rationale presented above, the longer copulation duration of satellite males could be explained by more intense genital stimulation, which may overcome female-imposed barriers to gain access to their gametes and increase males' fertilization success via cryptic female choice. For instance, in the damselfly *Ceriagrion tenellum*, whose males are not dimorphic, copulation duration is positively related to fertilization success, and this pattern is better explained by genital stimulation during copulation (Andrés & Cordero Rivera, 2000). A similar pattern has been recently reported for other species with non-dimorphic males, the pholcid spider *Holocnemus pluchei*: males with long copulation duration have more stored sperm in the female reproductive tract, even though males with short copulation duration transfer the same quantity of sperm (Cargnelutti, Calbacho-Rosa, Córdoba-Aguilar, & Peretti, 2018). Thus, future experimental studies with male-dimorphic species should investigate whether copulation duration of males exhibiting ARTs is longer than the time required for sperm transfer. By doing so, we can test the

hypothesis that these males perform longer genital courtship, and also that the prolonged genital courtship implies a greater number of offspring sired. An alternative hypothesis that cannot be discarded for several species included in our review is that males control copulation duration and males exhibiting ARTs spend more time removing sperm from the female reproductive tract (see Section 5.2).

Not only copulation duration may differ between male morphs, but also the sequence and types of behaviors recorded during copulation. A fascinating, but still poorly explored subject in studies on sexual selection in arthropods is the copulatory dialog, defined as a cooperative interchange of information between male and female during copulation (Peretti, Eberhard, & Briceño, 2006; Rodríguez, 2015). A well-studied case of copulatory dialog occurs in the pholcid spider *Physocyclus globusus*, in which non-dimorphic males stimulate the female during copulation by squeezing her abdomen with their robust pedipalps (Calbacho-Rosa & Peretti, 2015; Peretti & Eberhard, 2010; Peretti et al., 2006). While the male is squeezing the female, she may stridulate in response, and the probability of female stridulation increases when the pedipalpal squeeze is too long or when the male is not responsive to previous stridulations. Thus, the best copulatory courtship performed by a male does not imply more intense pedipalpal squeezes, but rather is the one that provides the proper intensity of squeezes tolerated by his partner. Males that are more responsive to female stridulation have greater fertilization success, suggesting that females have control over the fate of the sperm transferred by the males (Peretti & Eberhard, 2010; Peretti et al., 2006). Although there is no study on copulatory dialog in male-dimorphic arthropods, we anticipate differences in the communication between females and males of each morph during the copulation processes. These differences may emerge as consequence of the type and intensity of stimulatory behaviors exhibited by males of each morph, and also as a morph-specific female response to the stimulation received during copulation. This is an interesting possibility that could be explored with detailed observations of male-female copulatory interactions in species with long copulation duration and conspicuous stimulatory behaviors performed by males of both morphs. At this moment, however, detailed descriptions of copulatory courtship with non-intromittent structures are inexistent for male-dimorphic arthropods.

Even after copulation, behavioral differences between morphs should be expected. Prolonged spatial association with a female after copulation may benefit males by reducing her chances of accepting copulation with rival

males. Because mate guarding may reduce the level of sperm competition, males exhibiting this behavior should fertilize relatively more eggs than males that abandon their mates after copulation (reviewed in Alcock, 1994). Information on mate guarding is scarce for male-dimorphic arthropods, but there are some well reported cases. In the harvestman *Serracutisoma proximum*, a major male may remain in close proximity to a female for as much as 2 days after copulation. During this period, the female lays nearly 80–90% of her eggs in a clutch that will be attended by her for nearly 1 month; the remaining eggs are laid over the course of the following days. By mate guarding a female during the first 2 days after copulation, a major can increase his chance of fertilizing most of the eggs and can also reduce the copulation success of the minors that successfully invade his territory (Buzatto et al., 2011). Mate guarding can also increase fertilization success of territorial males in damselflies because this behavior may reduce the chances of sperm removal from the female reproductive tract by satellite males (Córdoba-Aguilar & Cordero-Rivera, 2008). In fact, territorial males of *M. costalis*, *M. nawai*, and *M. pruinosa* exhibit mate guarding behavior, physically securing the female while she oviposits, while nonterritorial males promptly abandon the female after copulation (Higashi & Nomakuchi, 1997; Nomakuchi, 1992; Watanabe & Taguchi, 1990). Finally, in the horned weevil *Parisoschoenus expositus*, both morphs guard females after copulation. There are intense male-male agonistic interactions during mate guarding, and large males usually repel smaller males (Eberhard & Garcia-C, 2000). We predict that in sites with high male density, the chances of a minor being repelled by a major is higher than in sites with low male density. This would lead to shorter mate guard duration for minors, and perhaps lower fertilization success (see discussion in Eberhard, 1983).

5.2 Genital differentiation between male morphs

In species with internal fertilization, as it is the case of all terrestrial arthropods, males face many challenges for successful fertilization. If females mate multiple times, males should (i) deliver sperm where they have the highest chance of fertilization (Eberhard, 1985), (ii) outcompete sperm from rival males (Simmons, 2001), (iii) induce female cooperation to bias the fertilization of her gametes (Eberhard, 1996), and (iv) overcome female-imposed barriers inside the reproductive tract (Arnqvist & Rowe, 2005). All these functions are often tightly associated with male genital morphology. In fact,

the three main mechanisms currently evoked to explain the morphological diversification of male genitalia are all related to sexual selection: sperm competition, cryptic female choice, and sexually antagonistic selection (reviewed in Eberhard, 2010a, 2010b, Hosken & Stockley, 2004 and Simmons, 2014). An in-depth review of these three mechanisms is beyond the scope of this paper. Our main goal here is to briefly highlight how each mechanism may affect genital diversification in males.

Male genitalia play an important role in sperm competition, and different traits are associated with the ability to gain precedence against rival sperm (i.e., sperm offense) and to resist rival sperm precedence attempts (i.e., sperm defense). The independence of traits influencing the offensive and defensive performance of male genitalia in sperm competition may contribute to inter-specific genital diversification (Hosken & Stockley, 2004; see Simmons, House, Hunt, & García-González, 2009 for an empirical example). Male genitalia can also be used as a courtship device, so that females may favor males with some genital traits that provide more effective stimulation during copulation or that fit better with female genital morphology. In this case, interspecific genital diversification is driven by cryptic female choice follow-ing a Fisherian sexual selection process (Eberhard, 1985, 1996). Finally, male genitalia can be used as a manipulative device that favors male's fertilization success but reduces female reproduction or lifespan (Arnqvist & Rowe, 2005). The sexually antagonistic selection may lead to interspecific genital diversification as a result of an evolutionary arms race between sexes for con-trol over reproduction as males and females struggle to maximize their own fitness (Arnqvist & Rowe, 2005).

The importance of sexual selection in promoting diversification of male genital morphology *between* species has already been demonstrated for sev-eral clades of insects and arachnids (e.g., Arnqvist, 1998; Cordero-Rivera & Córdoba-Aguilar, 2010; Eberhard, 2004; Kuntner, Coddington, & Schneider, 2009). At the species level, there is evidence linking quantitative variation in the size and/or shape of male genital structures and fertilization success (e.g., Arnqvist & Danielsson, 1999; Danielsson & Askenmo, 1999; House & Simmons, 2003; Otronen, 1998; Wenninger & Averill, 2006; Werner & Simmons, 2008). Thus, considering that the intensity and direc-tion of sexual selection acting on the morphology of male morphs usually differ (reviewed in Brockmann & Taborsky, 2008), can sexual selection also promote *within* species diversification in male genitalia? Despite the paucity of empirical data, we argue that the answer to this question is yes. For instance, males exhibiting a reproductive tactic based on sneak copulations

are expected to invest more in sperm competition because they usually mate with females that have already mated with territorial males (Parker, 1990; Parker & Pizzari, 2010). Thus, any genital trait that increases sperm offensive performance in sneaker males may increase their fertilization success. In turn, for territorial males, any genital trait that increases sperm defensive performance may reduce paternity loss to rival males. Therefore, different selective pressures promoted by sperm competition may lead to subtle or even discrete differences between male morphs in the morphology of their genitalia. These morphological differences may occur in the genitalia as a whole, but considering that the male intromittent organ of numerous terrestrial arthropods is composed of different parts (e.g., Eberhard & Huber, 2010; Wedell & Hosken, 2010), differences may also occur in specific structures that play a direct or indirect role in sperm competition. In fact, correlational data for some insect species in which males show continuous body size variation suggest that variation in male genital morphology influence male fertilization success via sperm competition (reviewed in Simmons, 2014).

To our knowledge, there is only one arthropod species in which genital differences between male morphs have been formally investigated, the dung beetle *Onthophagus taurus* (but see Kawano, 2004 for a comparison of allometric slopes of genitalic traits in male-dimorphic beetles). Male genitalia in this species are well described and formed by sclerites that vary in shape and complexity (reviewed in Simmons, 2014; Fig. 2A and B). More importantly, the functional role of the sclerites that form the male genitalia is known, so that male fertilization success is clearly related to variation in the shape of four out of five sclerites (House & Simmons, 2003). Specifically, sclerites 4 and 5 have a defensive role in sperm competition and are associated with the first male's ability to defend his paternity against a second male. Sclerites 1 and 2–3, in turn, have an offensive role in sperm competition, and are associated with the second male's ability to pre-empt the first male's paternity (House & Simmons, 2003; Fig. 2B). In an experimental study, House and Simmons (2007) varied the quality of the dung offered to the larvae and evaluated the condition dependent responses of several morphological traits in adult males of both morphs. The authors showed that, contrary to horn length, genital traits were unresponsive to differences in larval nutrition. However, regardless of the diet, all five genital sclerites were shorter in minors than in majors (House & Simmons, 2007). Thus, although male genitalia in *O. taurus* shows low levels of condition dependence and high levels of developmental canalization, there are marked differences between morphs in the size and perhaps shape of their genital sclerites.
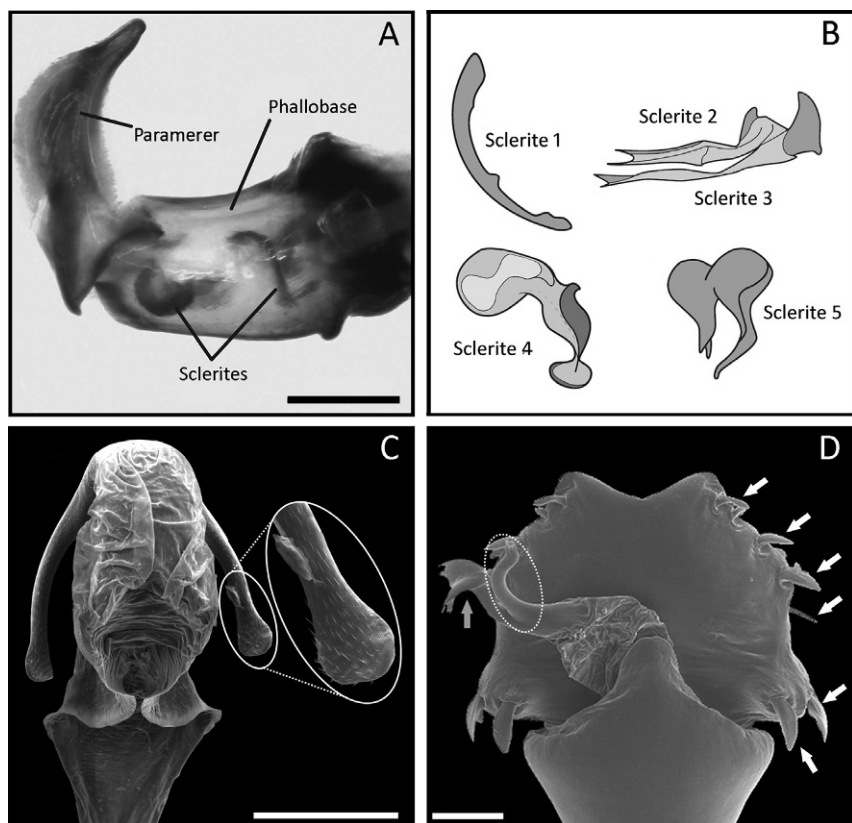
Fig. 2 (A) Male genitalia (aedeagus) of the dung beetle *Onthophagus taurus* that consists of two main parts: the phallobase, located apically, and the moveable hook-like parameres, located basally. Both parts are surrounding the enfolded endophallus that bears five sclerites visible through the phallobase. The endophallus rests invaginated inside the apical part of the aedeagus and is inflated and evaginated during copulation. Scale bar = 500 μm. (B) The five sclerites of *O. taurus* male genitalia are sclerotized parts of the endophallus membrane with different shapes and functions (modified from Werner & Simmons, 2008). Sclerites 1 and 2–3 (which seems to be a functional unit) have an offensive role in sperm competition, whereas sclerites 4 and 5 have a defensive role in sperm competition (House & Simmons, 2003, 2007). (C) Male genitalia of the male-monomorphic damselfly *Hypolestes hatuey* showing in detail the morphology of the spiny structure used by the males to remove sperm form the female's reproductive tract. Scale bar = 200 μm. (D) Male genitalia of the male-dimorphic harvestman *Serracutisoma proximum*. The white arrows indicate the right macrosetae, which possibly play a stimulatory role during intromsission, and the gray arrow indicates the dorsal process, which possibly plays a role in sperm removal from the female's reproductive tract (Macías-Ordóñez et al., 2010). Inside the dashed ellipsis is the ejaculatory duct, from which sperm is released. Scale bar = 50 μm. Photos by: (A) Leigh W. Simmons; (C) Adolfo Cordero-Rivera; (D) Márcio Bernardino da Silva.

These differences may explain why the fertilization success of minors, which supposedly are less attractive mates, is similar to that of majors (Tomkins & Simmons, 2000). Given that males of *O. taurus* do not access female spermatheca, where sperm are stored (House & Simmons, 2003), females are likely to be active participants in both offensive and defensive mechanisms. Thus, male genital traits used to stimulate female participation on sperm displacement should also be considered.

In several damselfly species, males have the ability to displace other males' sperm stored in the female reproductive tract. To do so, males use one of two alternative mechanisms (reviewed in Córdoba-Aguilar & Cordero-Rivera, 2005). The first one is the active removal of sperm, in which males use spines on the penis head to trap the sperm masses of rival males and bring them out of the bursa or even the spermathecae (e.g., Waage, 1979; Fig. 2C). The second mechanism is via sensory stimulation of female fertilization-related structures, in which males use aedeagal movements to stimulate the vagina where a number of mechanoreceptors are located. The sensory stimulation of these sensilla, which are used during fertilization and egg-laying, induces the female to eject sperm stored inside her spermathecae. Moreover, the wider the aedeagus, the more sperm is ejected by the female, probably because it favors better stimulation of female sensilla (Córdoba-Aguilar, 1999, 2002). These two mechanisms of sperm removal have been reported for several species with non-dimorphic males, and it is reasonable to suppose that they also occur in male-dimorphic species of the families Calopterygidae and Megapodagrionidae, such as those belonging to the genera *Mnais* and *Paraphlebia*, respectively (Hayashi & Tsuchiya, 2005). In this case, within-species divergence in male genital morphology may arise through female preference, sexual conflict over fertilization, and differences in the intensity of sperm competition faced by males of each morph. In *M. costalis*, for instance, both morphs have similar fertilization success (Tsubaki et al., 1997), indicating that non-territorial males are able to overcome potential disadvantages imposed by female preferences. In fact, non-territorial males have longer copulation duration (Siva-Jothy & Tsubaki, 1989a, 1989b; Table 1) and higher sperm displacement ability than territorial males (Córdoba-Aguilar & Cordero-Rivera, 2005). If higher sperm displacement ability exhibited by non-territorial males is caused by differences in genital morphology is an open question that deserves investigation. A testable prediction is that non-territorial males have more traits related to sperm removal, such as spines on the penis head or a wider aedeagus, which may lead to genital differences between male morphs.

Besides sperm removal, males of male–dimorphic species can use their genitalia to stimulate the female reproductive tract during copulation, thus inducing cooperation via cryptic female choice (Eberhard, 1996), and also to overcome potential barriers imposed by females inside the reproductive tract (Arnqvist & Rowe, 2005). If females show preference for males exhibiting the dominant reproductive tactic (e.g., female or territory defense), males exhibiting ARTs may increase their reproductive success if some structures in their genitalia are more effective in stimulating the female or overcoming female–imposed barriers. A selective pressure acting more intensively on the genitalia of males exhibiting ARTs may eventually lead to differences between morphs in their genital morphology. To our knowledge, this possibility has not been explored yet for any male–dimorphic arthropod species. An ideal study system are harvestmen, in which females frequently accept mating with males exhibiting ARTs (Buzatto & Machado, 2014). Sperm in harvestmen is aflagellate (Morrow, 2004) and, at least in species belonging to the suborder Laniatores, which concentrates most cases of male dimorphism, sperm cells are not directly deposited in storage organs inside the female reproductive tract (reviewed in Macías-Ordóñez et al., 2010). These particularities suggest that females have full control over the fate of the sperm they receive, and also that cryptic female choice plays an important role on male fertilization success (reviewed in Machado, Requena, Toscano-Gadea, Stanley, & Macías-Ordóñez, 2015). Moreover, the glans in many species belonging to the suborder Laniatores has macrosetae and other structures that probably interact with the female reproductive tract during copulation (Macías-Ordóñez et al., 2010; Fig. 2D). If cryptic female choice can promote divergence in the genital morphology of male morphs in harvestmen, we would expect differences in the shape and/or size of at least some of these structures that probably function as stimulatory devices.

As a final remark, it is important to stress that discriminating the relative importance of different sexual selection processes in genital evolution is difficult and this subject has been the focus of intense debate (Eberhard, 2010a, 2010b; Hosken & Stockley, 2004; Simmons, 2014). However, as we discussed in the examples mentioned above, each of these processes (i.e., sperm competition, cryptic female choice, and sexual antagonistic coevolution) have the potential to cause subtle or even marked divergence in the genital morphology of male morphs because each morph is likely subject to different selective pressures to achieve fertilization. In some species, sperm competition may have a predominant role, whereas in other species cryptic female choice or sexual antagonistic conflict may be the main drivers of

genital differentiation between morphs. In more complex cases, some structures in the male genitalia may respond to the selective pressure imposed by sperm competition, whereas other structures respond to female-imposed selective pressures, such as cooperation or antagonism (see Werner & Simmons, 2008 for a possible example). From a broader perspective, the investigation of within-species differences in male genital morphology may add further evidence on the role of sexual selection as one of the main drivers of genital diversification. Because both male morphs belong to the same species and males of each morph frequently copulate with the same females, any difference in the genitalia of the male morphs cannot be explained by the lock-and-key hypothesis, which proposes that genital divergence evolves as a form of hybridization avoidance (Eberhard, 1985).

6. Conclusions

Our review of the literature shows that, although male dimorphism is relatively frequent in insects and arachnids, there are few studies devoted to characterizing and comparing pre-copulatory and copulatory courtship behaviors between male morphs. However, the available information suggests that sexual interactions may show marked differences when females are paired with different male morphs. In some extreme cases, one morph courts the female before copulation whereas the other morph shows no courtship. Based on the empirical evidence synthesized in Table 1, we recognized four main processes that may lead to differences between male morphs in their pre-copulatory courtship behaviors. First, courtship may differ between morphs because only one of them expresses the traits used in pre-copulatory courtship, such as glands that produce nuptial gifts or stridulating organs. Second, differences between male morphs may be related to the costs of pre-copulatory courtship, so that only males of the morph in good body condition are able to pay these costs. Third, females may be more resistant to the copulation attempts of one male morph, which may increase their chances of being accepted performing longer of more elaborate courtship behaviors. Finally, when male–male agonistic interactions are intense, males of the smaller or less aggressive morph should abbreviate the courtship behavior to avoid interference or injuries imposed by males of larger and more aggressive morph. It is likely that other processes will be recognized in the future, when detailed qualitative and quantitative behavioral data are available for a wider range of species (see Peretti & Córdoba-Aguilar,

2007 for a discussion on the importance of fine-scaled behavioral observations in studies on sexual selection).

Some subjects on pre-copulatory courtship mentioned throughout our review and that deserve to be explored in future studies are:

- In Section 4.1, we showed examples of some male-dimorphic species in which females have marked mating preferences for males of the morph bearing sexually selected traits. This is the case of the calling morph in the black field cricket *Teleogryllus oceanicus* (Tinghitella & Zuk, 2009) and also the morph that offers nuptial gift in the spider *Oedothorax gibbosus* (Hendrickx et al., 2015; Vanacker et al., 2004). Mating preferences in these two species may be associated with indirect benefits, including good genes and attractive sons, or direct benefits, such as nutritious secretions from nuptial gifts (reviewed in Hunt & Sakaluk, 2014). However, males of the morph not bearing the sexually selected traits also achieve copulations and are maintained in natural populations. An interesting question that has not been explored is whether these males compensate their lack of attractiveness to females performing more intense alternative forms of pre-copulatory courtship, such as tactile stimulation and/or more elaborate kinetic displays. Such compensation does not necessarily imply that these males would be as attractive as males bearing the sexually selected trait, but simply that their mating probability would increase. The subject of behavioral compensation has received growing attention in the literature (reviewed in Dial, Greene, & Irschick, 2008), and male-dimorphic arthropods offer good opportunities for empirical studies.

- In Section 4.2, we discussed the case of the firefly *Luciola cerata*, in which adult size, number of lantern segments, and flashing rates differ between male morphs. These differences are probably related to the amount of food to which males had access during the larval stage because adults do not feed. To which extent similar carryover effects occur in polyphenic species in which males feed during adulthood is a question that deserves investigation. To address this question, future studies should manipulate food availability during development and quantify the intensity of pre-copulatory courtship behaviors exhibited by adult males of each morph. This type of experiment can bring information on the proximate causes of possible differences between morphs in the intensity of their pre-copulatory courtship behaviors. Moreover, mate choice experiments could investigate the connection between the intensity of these pre-copulatory courtship behaviors and male

mating success. We know that females of several non-dimorphic species evaluate mating partners based (at least in part) on the intensity of pre-copulatory courtship (reviewed in Byers et al., 2010). For male-dimorphic arthropods, experimental data are restricted to *Onthophagus* dung beetles, in which females also prefer males showing high rates of pre-copulatory courtship (Kotiaho, 2002). Therefore, further studies are necessary to test the generality of this pattern and understand whether differences in juvenile nutrition may translate into differences in courtship rates and copulation success among polyphenic arthropods.

- In Section 4.3, we described some cases in which differences in pre-copulatory courtship behaviors could be explained by female resistance to mating attempts of a given male morph. However, we stressed that in many male-dimorphic arthropod species, females apparently do not resist to the mating attempts of any male morph. In these cases, no marked differences in the pre-copulatory courtship behaviors of the morphs are expected to occur. However, the lack of female resistance to male mating attempts does not mean that females show no post-copulatory preference for one morph over the other. In fact, females may have full control of the fate of the sperm they receive and may accept sneak copulations for multiple reasons, including convenience polyandry. In these cases, paternity analyses could show the percentage of offspring sired by males of each morph. Despite the widespread use of molecular methods in current studies of sexual selection, we found only one paper with terrestrial arthropods (the dung beetle *O. taurus*) in which the relative paternity of the morphs was estimated (Simmons, Beveridge, & Krauss, 2004; see also Shuster, 1989 for an example with a male-trimorphic marine isopod). Paternity data on a wider range of species is important to understand if the mean fitness of the morphs differ. Moreover, using controlled experiments in the laboratory, paternity data can be used to explore how morphological and behavioral traits affect the fertilization success of males of each morph.

- In Section 4.4, we proposed the hypothesis that male-male agonistic interactions may abbreviate the pre-copulatory courtship duration of males of the smaller or less aggressive morph. This hypothesis accommodates the possibility of behavioral plasticity. In the same population, the risk of detection and injury may vary according to territory size, for instance. If small invader males can recognize the presence or proximity of large territorial males, they may adjust the intensity of pre-copulatory behaviors in response to the risks of being detected, interrupted, or

injured by the territory owner. When the perceived risk is high, invader males should abbreviate pre-copulatory courtship behaviors, but when the perceived risk is low, invader males should extent or exhibit more elaborate pre-copulatory courtship behaviors, which could increase their mating and/or fertilization success. An interesting prediction that emerges from this hypothesis is that, under natural conditions, the *variation* in the intensity of pre-copulatory courtship duration should be higher among males of the smaller or less aggressive morph than among males of the larger or more aggressive morph.

Males of different morphs may also differ in their copulatory courtship, including stimulatory behaviors outside and inside the females, but we could not find detailed data on this subject in our review. The only information reported in the studies refers to copulation duration, which may be related to sperm competition or cryptic female choice (e.g., Andrés & Cordero Rivera, 2000; Cargnelutti et al., 2018). In most cases in which quantitative data are provided, males exhibiting ARTs show longer copulation. As we discussed in Section 5.1, this pattern suggests that males exhibiting the sneaker tactic may perform more sperm removal and/or female genital stimulation when compared with males exhibiting the territorial tactic. By doing so, males exhibiting the sneaker tactic may outcompete sperm from territorial males, induce female cooperation to bias the fertilization of her gametes, and overcome female-imposed barriers inside the reproductive tract. Given that all these functions are performed by the male intromittent organ (Eberhard, 2010a, 2010b; Hosken & Stockley, 2004; Simmons, 2014), we suggested in Section 5.2 that sexual selection may lead to some degree of divergence in the genital morphology of male morphs. In fact, there is evidence for the dung beetle *O. taurus* indicating that genital sclerites directly involved in sperm competition differ in size and perhaps shape between morphs (House & Simmons, 2007). The possibility that sexual selection may lead to genital diversification not only between species, but also within species is an exciting idea that should be explored in additional male-dimorphic species. As pointed out by Arnqvist (1997), single-species studies focused on how variation in male genital morphology can affect fertilization success have tremendous potential to provide insights into the patterns and processes of genitalic evolution.

In conclusion, male dimorphism is perhaps one of the most emblematic examples of disruptive selection among animals (Brockmann & Taborsky, 2008). Understanding how and why male morphs differ in the pre-copulatory and copulatory courtship—two behaviors directly related to

male mating and fertilization success—may shed light on the maintenance of male dimorphism and also on the evolution of male genitalia, which remains as one of the most controversial subjects in evolutionary biology. Thus, we hope that the questions and ideas presented here stimulate an increase in quantitative studies on male-female interactions and male genital morphology in male-dimorphic arthropods, which are treatable study systems for both observational and experimental studies.

Acknowledgments

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