Chapter 4
The Choice of Sexual Partner in Social Wasps

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Abstract In many animals, females (and sometimes males) are more or less choosy in relation to what type of partner to mate. This intersexual selection favors traits that make individuals sexually attractive. Traditionally, social insects have mostly been the targets of sociobiological studies, but the exciting recent literature on ants, bees, and wasps has provided a lot of insights about how sexual selection shapes the reproductive behavior and also the social organization in insect societies. In this chapter, we discuss the reasons why wasps are good models for studying sexual selection. In addition, we describe the different criteria that wasps use during the mate choice. Finally, we highlight future directions to extend knowledge about how sexual selection shapes the choice of the sexual partner in these insects.

Keywords Sexual selection · Mate choice · Visual signals

4.1 Introduction

The selection of a sexual partner is an important aspect of animal life. Technically speaking, it is referred to as intersexual selection. Throughout this process, traits that improve the probability of an individual to be chosen by the opposite sex as a sexual partner are favored. Intersexual selection is one of the two components of the theory of sexual selection (the other one is intrasexual selection) proposed by Darwin in 1871. Such a phenomenon, which has already been studied in various animals (reviewed by Andersson and Iwasa 1996), can result in the evolution of more or less choosy species in relation to what type of partner they mate.

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Although well studied at a certain rate, sexual selection in social insects has received relatively little attention. This is probably due to the impact of the early contributions of Hamilton (1964a, b) as well as Trivers and Hare (1976), which motivated numerous sociobiological investigations focused on female cooperation. Their studies have marked the development of the theory of kin selection as the basis for explaining how helping behavior can be favored by natural selection and receiving since then widespread support (Queller 2016). As a result, investigations about sexual selection in social insects have fallen into the background. Nevertheless, more recent studies, including those with social wasps, have shown that sexual selection has shaped several traits of these insects, including different criteria for sexual partner choice (described below).

The perception about the importance of studying sexual selection in social insects has motivated a growing number of investigations, resulting in excellent reviews on the subject (Strassmann 2001; Baer 2003; Boomsma et al. 2005; Baer 2014; Beani et al. 2014; Baer 2015; Heinze 2016). In this chapter, we focused on *Polistes* paper wasps (but also some other wasps) to (i) discuss the reasons why wasps are good models for studying sexual selection, (ii) describe the different criteria that wasps use during the mate choice, and (iii) highlight some future directions to extend knowledge about how sexual selection shapes the choice of the sexual partner in these insects.

4.2 Social Wasps as Models for the Study of Sexual Selection

In studying sexual selection, model species must be able to be observed in the field since the main objective is to understand how the mechanism of selection works in the natural environment where species evolve and acquire their traits. Well-controlled experiments that can only be done in the laboratory may then be interpreted against a solid framework of ecology, selective pressures, and adaptations of the species to its natural evolutionary context (Andersson and Simmons 2006). *Polistes*' life cycle is relatively well known (Fig. 4.1), and the general pattern of sexual behavior in at least some species can be observed in the field (Beani et al. 1992). Typically, males are bred in late summer, they stay only for a few days in the colony, and then, they disperse to find sexual partners. Male aggregations are observed, repeatedly visiting conspicuous areas (= *landmarks*) and sunny places, comprising "meeting points" where females visit and mate. Interspecific differences in sexual behavior are observed regarding the occurrence of defense of territories and the degree of aggression among males. Thus, the *Polistes* mating system ranges from swarms of little-aggressive males which collectively patrol common routes and do not defend territories to *leks* formation, in which highly aggressive males defend individual territories against cospecifics. Male sexual behavior in some *Polistes* has been reviewed by Beani (1996). Females, in turn, generally mate only with one male (monandric; Strassmann 2001) for a short time after their emergence – they never copulate again! Female multiple mating (polyandry) is observed

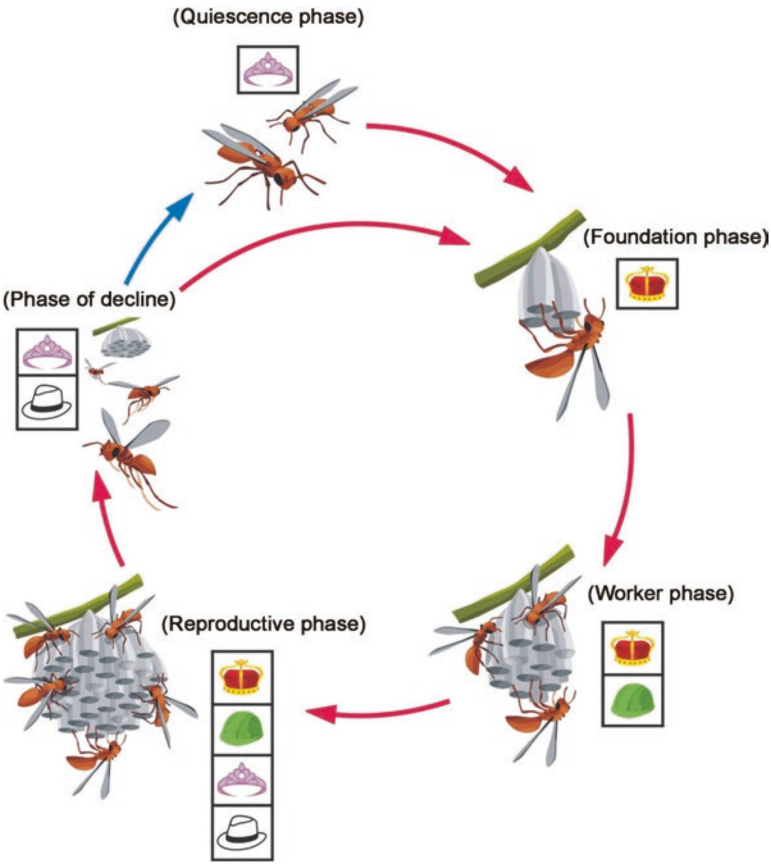

Fig. 4.1 Typical colonial cycle of *Polistes versicolor*. *Foundation phase:* The cycle begins when environmental conditions are favorable (red arrows). At this stage, a female initiates the foundation of a nest (alone or cooperatively). Oviposition occurs immediately after the construction of each nest cell by the founder (crown icon), which performs, in addition to oviposition, all maternal behavior (foraging, feeding the larvae, building, and nest defense). *Worker phase:* The first female offspring are female workers (helmet icon). These individuals remain in the colony and assume all maternal behavior, while the female founder, now called queen, is devoted mainly to oviposition. *Reproductive phase:* After producing several generations of workers, the colony also produces males (hat icon) and potential future queens, also called potential founders or *gynes* (icon tiara). These reproductive forms leave the colony to mate; males leave the colony permanently while females return. *Phase of decline:* Reproductive forms still emerge (to a lesser extent), but the queen and workers die, and little by little the nest runs out of immature forms. Even at this stage, if environmental conditions remain favorable, potential future queens leave the colony where they were raised to start their own colonies, becoming founders and then queens. If environmental conditions are no longer favorable (blue arrow), potential future queens enter the *quiescence phase:* Potential future queens remain in a kind of reproductive pause, sheltering in their own nest or in weather-protected cavities until favorable environmental conditions return when the foundation phase begins. The colonial cycle lasts from 3 to 10 months. The reproductive roles of the castes are flexible. For example, subordinate females in cooperative foundations (foundress association) may behave as workers. Also, a worker can replace the queen in case of her death or disappearance (nest inheritance). Data on the natural history of *P. versicolor* was obtained from Gobbi et al. (2006) and references cited by them. The cycle design was adapted from Hunt et al. (2011)

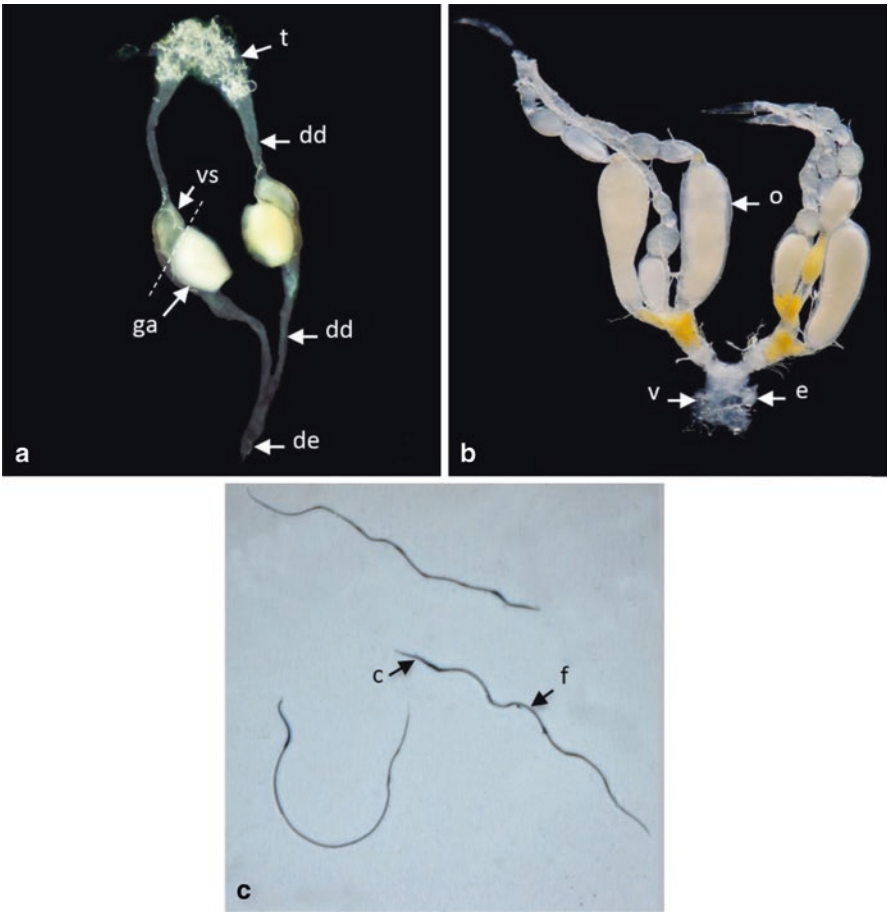

Fig. 4.2 Reproductive systems and sperm of *P. versicolor*. (**a**) Reproductive system of the sexually mature male: Sperm are produced in the testes which degenerate during sexual maturity (t). Sperm migrate through the anterior portion of the vas deferens (dd) to the seminal vesicles (vs), where they are stored until ejaculation. Afterwards, the accessory glands (ga) are inserted. Their content along with the sperm compose the ejaculate which passes through the posterior region of the vas deferens to the ejaculatory duct (de). (**b**) Reproductive system of the sexually mature female: Sperm obtained during copulation are stored in a specialized region, connected to the vagina (v), called spermatheca (e). Oocytes (o) develop as they approach the vagina, and as they pass through it, fertilization may occur. (**c**) Sperm obtained from seminal vesicles of a sexually mature male. After hematoxylin staining it is possible to discriminate the head (c) and flagella (f) of each sperm

in some *Polistes* species (Seppä et al. 2011; Southon et al. 2019). Inseminated females store sperm in a specialized organ, the spermatheca (Fig. 4.2). These sperm are used to produce several generations of workers and, at the end of the colonial cycle, reproductive females (potential future queens, also called gynes). Males are produced from unfertilized eggs (parthenogenesis).

In addition, the sexual behavior of *Polistes* can be studied in large cages (Beani and Turillazzi 1988; Beani and Zaccaroni 2015) and also in small glass arenas (Liebert et al. 2010; Izzo and Tibbetts 2012; de Souza et al. 2014), which allows well-controlled observations and experiments.

Model species should also have conspicuous sexual dimorphism, as this is an evidence of strong sexual selection (Andersson and Simmons 2006). *Polistes* have several sexually dimorphic characteristics. For example, males and females have body color patches with different sizes and shapes (Izzo and Tibbetts 2012; De Souza et al. 2014; Cappa et al. 2016; De Souza et al. 2016), and some of these patches are larger and more variable in males than in females. Below it is described how such body patches comprise sexually selected signals mediating the choice of the sexual partner.

In addition to the factors mentioned above, particularities related to the sex determination system, the effect of kinship relations on the social dynamics of the colonies, and the differences in the reproductive potential of females make *Polistes* wasps excellent models to investigate how selection has shaped the choice of the sexual partner.

4.3 Criteria for Selecting a Sexual Partner

The criteria for choosing a sexual partner in *Polistes* social wasps are slowly being unveiled, as we know.

4.3.1 Kinship

In Hymenoptera in general, males are haploid and females diploid. In these insects, normal female development requires heterozygosity at one or more specific *loci*, constituting the complementary sex determination mechanism (Whiting 1943; Crozier 1971; Whiting 1924; Van Wilgenburg et al. 2006). Therefore, mating between highly related individuals (e.g., between siblings) can result in the production of genetic “errors” known as diploid males. Diploid males are produced when diploid individuals are homozygous for one or more sex-related *loci* (Fig. 4.3) (Whiting 1933). These individuals would normally be females, but due to homozygosity, they develop in males. Diploid males impose fitness costs on colony productivity because they consume resources but are typically sterile (Liebert et al. 2004). Because of the costs of incestuous copulation, natural selection should favor behaviors that prevent its occurrence. In this sense, copulation between closely related individuals can be prevented by (i) intersexual nestmate recognition and subsequent rejection of related partners and/or (ii) a mechanism that minimizes the likelihood of finding a sexual partner closely related.

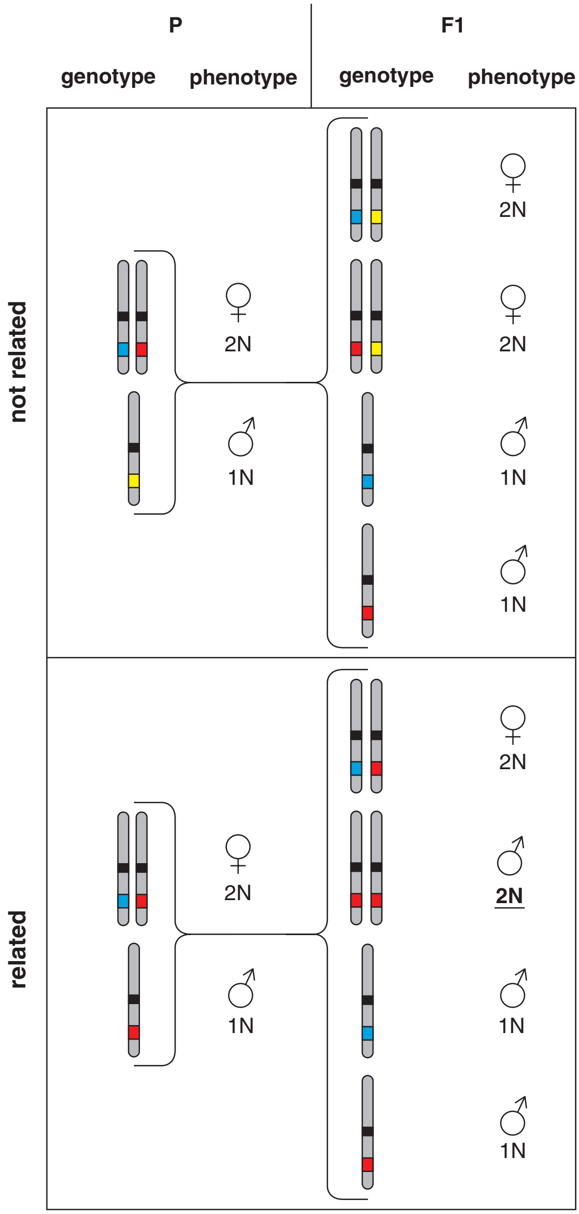

Fig. 4.3 Chromosomal representation of the complementary sex determination system in Hymenoptera, where males are typically haploid (1 N) and females are diploid (2 N). Note that in this scheme, sex is determined by a single *locus* with multiple alleles (colored regions on chromosomes) in a population. Heterozygosity results in a female phenotype, and the hemi- or homozygosity produces a male phenotype. Crossbreeding between siblings can result in the production of diploid (**2 N**) males which do not contribute to colonial productivity and are functionally sterile

Same-sex nestmate recognition has been well studied in *Polistes*. Both males and females are known to possess such ability (Shellman-Reeve and Gamboa 1985; Ryan and Gamboa 1986; Starks et al. 1998). This recognition is based on colony-specific chemical signatures determined by a unique combination of hydrocarbons present in the cuticle of individuals and also on the surface of nests (reviewed by Gamboa 2004; see Chap. 11 on cuticular hydrocarbons). The ontogeny of nestmate recognition may involve a number of mechanisms (Cappa et al. 2020). Thus, by recognizing such combinations of hydrocarbons, wasps would be able to avoid copulation with related sexual partners. However, evidence of intersexual nestmate recognition and subsequent nestmate avoidance has been demonstrated only for *Polistes fuscatus* (Ryan and Gamboa 1986), in which controlled behavioral trials have shown that copulation between relatives is less frequent compared with those between unrelated individuals. The other species of wasps studied do not seem to avoid copulation with related sexual partners (*Polistes*, Liebert et al. 2010; Beani and Turillazzi 1988; De Souza et al. 2017a; *Ropalidia*, Sen et al. 2010; Shilpa et al. 2010), even when they are able to discriminate related and unrelated sexual partners (Liebert et al. 2010). This suggests that the absence of sexual preference does not result from a limitation in the discriminatory ability. So how do these species deal with the possibility of incestuous copulation? As stated above, incest can also be prevented through a mechanism that minimizes the likelihood of finding a related partner. Copula in *Polistes* occurs predominantly outside the nest, constituting a mechanism that can help to prevent incest. In addition, emerging males are still sexually immature, as it takes a few days for the sperm to migrate from the testes to the seminal vesicles (Fig. 4.2a). Thus, eventual copulations with newly emerged males, sometimes reported, are unlikely to result in insemination. Also, males, leaving the colony, take on a nomadic life when they seek females to mate. This removal from the colony may also decrease the occurrence of incest. Sometimes the colony may specialize in producing only reproductive males or only reproductive females, thus avoiding incest. Finally, in the population, virtually all reproductive males and females are produced at a relatively short interval in summer, resulting in many potential sexual partners. This type of reproductive assembly results in low likelihood of mating between related sexual partners. This set of biological, ecological, and behavioral traits is believed to relax the selection of sexual partner in relation to kinship (De Souza et al. 2017a).

But after all, do wasps actually avoid incestuous copulation? Diploid males, a consequence of mating with related partners, have not been found in native social wasp populations (Liebert et al. 2006; Nagamati Junior et al. 2010). This suggests that the above mechanisms are effective in preventing incest among these insects. However, diploid males have been reported in invasive populations (Liebert et al. 2006), suggesting the occurrence of copulation between relatives. Incest may be common in early invasive populations, especially when small and highly related, thus, reflecting low allelic diversity. Nonetheless, it is also seen as an adaptive form so that under those conditions, some female offspring are produced until allelic diversity increases (Liebert et al. 2010).

4.3.2 Number of Partners

In female social Hymenoptera, the number of sexual partners varies according to a number of costs and benefits (Strassmann 2001). In *Polistes* and *Ropalidia* females are typically monandric (Strassmann 2001), resulting in a high degree of kinship among colony members (compared to polyandric females). Of note, low and high polyandry have evolved in a few *Polistes* (Seppä et al. 2011; Southon et al. 2019). Monandry enhances social harmony, because the greater the relationship between cooperating females, the greater the indirect fitness obtained (inclusive fitness theory; Hamilton 1964a, 1964b). As a result, helper females emerged from monandric colonies have more to gain (mean sister relationship = 75%) compared to females emerged from polyandric colonies (mean sister relationship <75%). High kinship is especially important for fostering harmony in primitively eusocial groups. This is because reproductive and non-reproductive females are totipotent and can behave as a helper, start their own colony, or even reproduce directly in the colony where they were born, if there is an opportunity.

In the highly eusocial wasps Vespinae, queens can be monandric or polyandric, as the morphological difference between breeding and non-breeding females is so pronounced that workers lose the ability to start their own colony. Wasp polyandry results in increased genetic polyethism (allowing a more efficient division of labor) and colonial immunity (Saga et al. 2020), which is especially important due to the large number of genetically similar individuals in highly eusocial insect colonies. It also promotes policing among workers, preventing them from laying eggs that would give rise to males, thus favoring queens (Strassmann 2001; Crozier and Fjerdingstad 2001). These benefits of polyandry have been described for highly eusocial wasps, but whether they also hold for *Polistes* is unknown.

Primitively eusocial wasp males, such as *Ropalidia*, follow the male stereotype and can fertilize several females (polygyny) (Shilpa et al. 2012). This ability is especially important for these primitively eusocial wasps, since not all inseminated females will in fact be queens. When a single female starts a colony, she will be the queen of this colony. However, when the colony is started by more than one female, a dominance hierarchy is established. Then, one or a few individuals hold all or most of the direct reproduction (functional queens), while the others have little or no participation in oviposition (functional workers) (*Polistes*: De Souza et al. 2008; Grazinoli et al. 2010). Thus, mating with a future foundress does not guarantee reproductive success. Nevertheless, polygyny may increase the chances that at least some females will use sperm. Male multiple mating (polygyny) likely holds for *Polistes* as well, but it remains to be investigated.

4.3.3 Caste

In primitively eusocial wasps, the reproductive output can differ dramatically among females in the same colony, despite they are all morphologically simillar and reproductivelly totipotent (De Souza et al. 2008; Grazinoli et al. 2010). Queens tend to assume most direct reproduction (principal egg layers), while workers tend to assume non-reproductive roles (e.g., foraging or nest defense). Since males produce a limited amount of sperm (the testes degenerate after sexual maturity; Fig. 4.2), they are expected to be able to discriminate and avoid copulation with female workers. Inseminated *Polistes dominula* females begin the foundation of colonies in spring, producing several generations of workers, and by the end of summer, they also produce reproductive forms (males and potential future queens). A few days after emergence, males leave the nest and congregate in *lek* aggregations at strategic points located in areas of high wasp density (Beani and Turillazzi 1988). During this period, future founders, still virgin, visit the *leks* to mate, while workers forage near the *leks* increasing the chances of their encounter with males (Beani and Turillazzi 1988; Beani 1996). Therefore, males can interact with both future founders and workers. In studying the sexual behavior of males in the laboratory, Cappa et al. (2013) showed that they discriminate castes, preferring to court future foundresses (future queens). Such behavior is presumably adaptive, especially since after the mating season (late summer), females hibernate for a few months before starting the new colonies. As foundresses usually survive the weather conditions in winter and workers do not, the sexual preference of *P. dominula* males seems to be a mechanism to ensure copulation with more appropriate sexual partners.

4.3.4 Ornaments

The use of ornamentation as a criterion for choosing a sexual partner in social wasps is one of the most recently studied topics. Neotropical wasp males *Polistes simillimus* have a black spot on the vertex around the ocellae (Fig. 4.4). This spot is sexually dimorphic, being always small and slightly variable in females, but highly variable in males (Fig. 4.4). Experimentally speaking, when wasps interact in a small arena, males with a higher proportion of black pigment are more likely to be chosen as sex partners. Likewise, males experimentally manipulated to have higher black pigmentation are preferably chosen as a sexual partner over males manipulated to have lower proportion of black pigmentation. This means that *P. simillimus* females discriminate these spots during the choice of sexual partner (De Souza et al. 2014). Such ornaments are considered signs of quality as they are associated with the male’s immunocompetence and longevity (De Souza et al. 2018).

Similar behavior has been previously reported for the social wasp of the temperate region, the *P. dominula*. Males have a pair of yellow abdominal spots, located on the lateral surface of the second abdominal tergite (Izzo and Tibbetts 2012; De Souza et al. 2017b; De Souza et al. 2020). Such patches are always small and round in females, but in males they range from round to extremely irregular ones. When wasps interact in a small arena, males with rounded spots are more likely to be selected by the females. This same result is also observed when spots on males are experimentally manipulated, characterizing them as sexual ornaments. Such ornaments are considered signs of quality as they are associated with the male’s fighting ability (Izzo and Tibbetts 2012), territory holding (Beani et al. 2019) and nutrition during the larval period (Izzo and Tibbetts 2015).

Fig. 4.4 Variation in the proportion of black pigment in male (above) and female (below) heads of *P. simillimus*. Note that males have larger and more variable spots than females

4.4 Future Directions

Despite the growing number of publications related to sex partner choice in *Polistes* social wasps, there is still much to understand. Here are some promising topics:

1. In several species from temperate places, females have visual signals of quality used to mediate aggressive interactions related to the intracolonial dominance hierarchy (Cervo et al. 2015). These signs are known to be good predictors of survival, reproductive success, and rank (Tibbetts et al. 2015). Although these signs have presumably evolved in a female-female context, it is possible that males will preferentially discriminate and mate with females whose visual signals indicate high quality and have greater reproductive success.
2. It has been seen that the preference of males for future foundresses rather than workers in a temperate species (Cappa et al. 2013) seems to be an adaptation to acquire mating with more appropriate females (since workers do not survive to found new colonies after winter). But, what about such preference in neotropical species? In these regions winter is not harsh, so workers can survive to found new colonies.
3. How to explain the preference of females for sexual partners with certain ornaments (Izzo and Tibbetts 2012; De Souza et al. 2014) when apparently males offer nothing but the ejaculate? Possibly, females could choose mates with better reproductive potential if the ornaments indicate quality ejaculate. This hipothesis was recently addressed in *P. dominula* (De Souza et al. 2020) providing negative results.

4. Quality signals, which reflect physiological and ontogenic aspects of individuals (Tibbetts 2010; Izzo and Tibbetts 2015), are known to be affected by the presence of parasites (Tibbetts et al. 2011). So, is male sexual ornamentation also altered by parasitism? This hypothesis was recently addressed in *P. dominula* (De Souza et al. 2020) also providing negative results.

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