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Males do not like the working class: male sexual preference and recognition of functional castes in a primitively eusocial wasp

F. Cappa^{a,*}, C. Bruschini^a, R. Cervo^a, S. Turillazzi^{a,b}, L. Beani^a

^aDipartimento di Biologia, Università degli Studi di Firenze, Firenze, Italy

^bCentro Interdipartimentale di Spettrometria di Massa, Università degli Studi di Firenze, Firenze, Italy

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Discrimination among potential partners is a critical step in sexual selection to avoid wasting reproductive resources on an unsuitable mate. In the female-dominated hymenopteran societies males have often been regarded as 'flying sperm containers' spending all their time and energy in trying to acquire a mate. We investigated the male sexual preference for potential partners using as a model the primitively eusocial wasp *Polistes dominula* in which female caste is rather flexible and difficult to determine. By means of laboratory bioassays, we compared the males' behaviour towards females of different reproductive potential. Males were able to recognize female castes, strongly preferring reproductive females to workers, regardless of female age or health. The results show that in this species caste plays a key role in orienting male discrimination and preference, presumably through chemical cues, towards reproductive females both healthy and parasite-castrated. Overall, our study shows that social Hymenoptera males are not always 'small mating machines' eager to mate.

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Sexual selection stereotypes of female 'choosiness' versus male 'undiscriminating eagerness' to mate (Knight 2002; Andersson & Simmons 2006; Hosken & House 2011) represent the typical theoretical framework for mate choice. However, even males face costs during mate choice in terms of both energetic investment and risk of choosing a mate that does not guarantee increased fitness (Dewsbury 1982; Wong & Jennions 2003). A differential male sexual preference towards potential female mates is predicted to evolve in systems in which male mating effort or parental investment is high (Burley 1977; Gwynne 1981, 1991; Jones & Hunter 1993) or in response to a large variation in female quality, especially when 'mate availability' exceeds male 'capacity to mate' (Kvarnemo & Simmons 1999; Bonduriansky 2001; Edward & Chapman 2011).

This last scenario represents the case of some species of primitively eusocial insects, in which males encounter females belonging to different castes based on physiological status, which might differ considerably in their reproductive potential (Wheeler 1986; O'Donnell 1998). In the female-centred hymenopteran societies males have often been regarded as merely short-lived 'flying

sperm containers' (Baer 2003). Produced only for a brief period of time during a specific phase of the colony cycle, with rare exceptions (Yamauchi et al. 1996; Heinze et al. 1998; Sen & Gadagkar 2011), after reaching sexual maturity they depart from their native colonies, never to return. Their fate in terms of reproductive success is often constrained by a limited supply of sperm and female monogamy (Thornhill & Alcock 1983; Strassmann 2001; Boomsma et al. 2005). Males of social Hymenoptera would benefit from the ability to distinguish between reproductive and nonreproductive females. Assessing a female's reproductive value could be particularly difficult, however, for males of the more primitively eusocial species, such as the paper wasps of the genus *Polistes*, characterized by morphologically similar and relatively flexible castes (Strassmann 1981; Sumner et al. 2006; Hunt et al. 2007).

The paper wasp *Polistes dominula*, a model organism for sociobiology studies (Turillazzi & West-Eberhard 1996), provides excellent opportunities to test the evolution of male sexual preference according to female quality and recognition of functional female castes. During the annual colony cycle, fertilized females (i.e. foundresses) leave their winter shelters in spring and establish new nests; workers start to emerge at the end of spring and, until autumn, they are active on nests, assuming the duties of foraging, nest construction and colony defence; reproductive individuals (i.e. sexuals) emerge in summer (Pardi 1943,

* Correspondence: F. Cappa, Dipartimento di Biologia, Università degli Studi di Firenze, via Madonna del Piano, 6, 50019, Sesto Fiorentino (Firenze), Italy.
 E-mail address: federico.cappa@unifi.it (F. Cappa).

1996). A few days after eclosion males leave their nests to gather in lek-like aggregations at landmarks strategically located in areas with high wasp density (Beani & Turillazzi 1988). At this time foraging activity in the surroundings of leks, which often include resources, increases the chances of encounters between courting males and foraging workers, while virgin reproductive gynes (i.e. future queens) visit leks to mate (Beani & Turillazzi 1988; Beani 1996).

Worker mating is reported in various species of *Polistes* (Strassmann 1981; Suzuki 1997, 1998; Reeve et al. 1998); thus, workers can be potential partners for males. Nevertheless, given the absence of conspicuous morphological differences between workers and gynes, the inability of *P. dominula* males to discriminate between the two groups of females might be a problem for a number of reasons. First, males would have a return in terms of direct fitness only by mating with a worker that has a dominant position on its nest (Monnin et al. 2009). Moreover, because the vast majority of workers will die at the end of summer, mating with a worker may be beneficial for males only if it occurs in an early phase of the colony cycle when workers might still be able to produce their own offspring given the opportunity. Finally, *P. dominula* males spend weeks or even months at leks waiting for potential partners ('the marathoner hypothesis' see Beani 1996) but their chances of reproduction are constrained by a fixed complement of sperm (M. Gottardo, F. Cappa, F. Manfredini, R. Dallai & L. Beani, unpublished data). Therefore, we expect males to discriminate between gynes and workers, since male reproductive efforts directed towards the latter might be a waste.

Moreover, even *P. dominula* gynes may vary in their reproductive quality or value as the species is the primary host for the parasite *Xenos vesparum* (Strepsiptera, Xenidae). Among the morphophysiological changes induced by the parasite, the most dramatic is the castration of female hosts (Strambi et al. 1982; Beani et al. 2011). Infected females aggregate near leks, where the parasite mates (Beani et al. 2005), increasing their chances of encountering sexually active males. Thus, discriminating between healthy fertile and parasite-castrated gynes should also be beneficial for males because only the former will be able to reproduce the following season.

We investigated the *P. dominula* male's ability to recognize workers and future queens and its sexual preferences despite the morphologically similar and flexible castes of this species. We also tested the male's preference towards gynes with a different reproductive potential by exploiting the natural manipulation induced by the castrating parasite *X. vesparum* on its female hosts. We carried out two sets of male preference trials: the first experiment simulated natural conditions, that is, we studied males active at leks and females collected from field colonies, while for the second we used individuals eclosed from laboratory colonies, to control for age and mating experience of both males and females.

METHODS

Collection and rearing of wasp colonies

Colonies of *P. dominula* were collected in August 2010 ($N = 20$) and June 2011 ($N = 60$) from six different sites in Tuscany, Italy. Nests were transferred to the laboratory, placed in nestboxes (cubic glass cages of $15 \times 15 \times 15$ cm), and provided with ad libitum water, sugar and fly maggots. The wasps found on the nest at collection as well as newly eclosing individuals were marked with Testor's enamel paint. All the emerging males were removed daily from each colony.

Selection of female wasps

Female wasps from the colonies collected in the field at the end of the colony cycle during 2010 were classified as (1) workers: females present on the nest at collection with evidence of wing wear as an index of foraging activity (Toth et al. 2009); (2) healthy and parasite-castrated gynes: last-generation females eclosing in the laboratory at the end of August, either healthy or naturally infected by the parasitic castrator *X. vesparum* extruding from the abdomen. Female wasps reared in the laboratory from nests collected in 2011 were classified as (1) workers: first generations of females eclosing from 36 pre-emergence colonies, that is, with only foundresses and immature offspring, before the emergence of male offspring; or (2) gynes: females eclosing from 24 post-emergence colonies, collected in warmer plain areas where the colony cycle is enhanced, after the emergence of the first cohort of males. Colonies were collected at different stages of the cycle to obtain reproductive gynes from postemergence nests along with first generations of female workers from pre-emergence colonies. All female wasps ($N = 180$) used in our experiments were at least 2 weeks old to allow all the wasps to develop their full cuticular hydrocarbons (CHCs) profile (Lorenzi et al. 2004). The age difference between females presented to each male was less than a week. The range of female age was between 2 and 4 weeks. After the experimental trials, females were killed by freezing and then dissected for accurate caste assignment.

Selection of sexually active males

Males ($N = 150$) were collected at the end of August 2010 from five different natural lek systems located in the surroundings of Florence and housed in the laboratory with ad libitum water and sugar. In 2011 males ($N = 61$) removed from postemergence colonies were housed with ad libitum water and sugar. For behavioural assays we selected a sample of males for each year (2010, $N = 40$; 2011, $N = 30$) based on a similar body size measured as the maximum head width of males (Eickwort 1969). Only mature males of at least 3 weeks of age (seminal vesicles full of sperm, M. Gottardo, personal communication) and comparable size (head width measured with a calliper to the nearest 0.01 mm; the head width chosen was 3.60 mm) were used in the experimental trials.

Behavioural assays

To assess the male's ability to recognize and selectively prefer females of different reproductive value, in our first experiment we tested male sexual preference by sequentially presenting every male ($N = 40$) with three females that differed in reproductive potential. Each male was presented in a random order with a worker (W, $N = 40$), a healthy gyne (HG, $N = 40$) and a parasite-castrated gyne (PG, $N = 40$) from different nests. Each session consisted of a set of three consecutive 5 min videotaped (Digital Video Camera Recorder, Sony DCR-SR35E) trials, with a 2 min interval, during which every male was paired with one female in an observation arena (10 cm diameter petri dish). We chose this small arena and short trial duration compared to previous studies (Liebert et al. 2010; Sen et al. 2010; Shilpa et al. 2010; Izzo & Tibbetts 2012) because we wanted to evaluate the male's ability to assess rapidly the reproductive quality of a potential partner. In natural leks male–female encounters are usually brief (Beani 1996); therefore a quick assessment of a female's reproductive value might prevent the male from mating with low-quality partners. We deliberately chose to present males with females of different size to assess any possible male preference for this trait.

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