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Review article

The rarity of multiple mating by females in the social Hymenoptera

J. Strassmann

Department of Ecology and Evolutionary Biology, MS 170, Rice University, P. O. Box 1892, Houston TX 77251, USA, e-mail: strassm@rice.edu

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Summary. Interest in how often female social insects mate is particularly intense because of its impact on sociality and because of the well-known extreme multiple mating in honeybees. With multiple mating, worker to brood relatedness decreases but worker versus queen interests often converge. The overwhelming majority of species of social ants, bees, and wasps mate only once. Even those species where some females mate multiply typically have effective mate numbers close to one. Ants have effective mate numbers of 1.43, which drops to 1.15 if the advanced fungus growers (2.14) and harvester ants (6.76) are excluded. Honeybees have effective mate numbers of 12.48. Stingless bees and bumblebees have effective mate numbers of only 1.06 and 1.02 respectively. Polistine wasps have effective mate numbers of 1.01. Vespine wasps have effective mate numbers of 1.12 excluding only *Vespula* which has effective mate numbers of 3.68. Favoring the very low mate numbers we observe for nearly all female social insects is the narrow time window for mating, lack of material gain from males, lack of male ability to harass females (who must move their sting aside to mate in most species), and lack of paternal care. Single mating may be further favored by the apparent lack of any post-copulatory sperm discrimination mechanisms. Leks and male territories, which are common in social insects, make it easier for females to choose the single best mate, further contributing to low mate numbers. Multiple mating is a rare, derived trait in a generally single-mating group. Single mating may have facilitated the origins of sociality in the Hymenoptera because it confers higher relatedness among potential workers and the brood they care for. The rare exceptions to low mate numbers all come from highly social species with single queens, morphological castes, and many workers. Multiple mating might be stable in highly social species because their highly specialized workers have few selfish responses to lowered relatedness. The unusual cases of multiple mating are most likely to be selected for because they increase genetic diversity in the brood, though empirical support for specific genetic diversity hypotheses has proved to be elusive. What is clear is that single mating is predominant in this large, evolutionarily and ecologically successful group.

Key words: Multiple mating, polyandry, social conflicts, Hymenoptera, genetic diversity.

Introduction: why females mate more than once

The realization that females of many species from chimpanzees (Gagneux et al., 1999) to pseudoscorpions (Zeh and Zeh, 1994) mate more than once has stimulated much investigation into possible advantages (e.g. Thornhill and Alcock, 1983; Eberhard, 1985, 1996; Andersson, 1994; Gowaty, 1994; papers in Choe and Crespi, 1997; papers in Birkhead and Møller, 1998; Arnqvist et al., 2000; Arnqvist and Nilsson, 2000; Jennions and Petrie, 2000). Postulated gains to females that mate multiply include (1) need for more sperm, (2) material gains, (3) costs of avoiding males, (4) difficulties in identifying the best male, (5) genetic compatibility issues, (6) difficulties of access to the best possible male, and (7) advantages of a genetically diverse brood.

The most basic asset acquired by females at mating is sperm to father their progeny. It is possible that under some circumstances sperm could be limiting. There should be strong selection for individual males to provide all the sperm a female needs, but males that have already mated with other females may have depleted their sperm reservoirs, particularly if sperm is not replenished in adulthood.

Material gain may take the form of nuptial gifts or nutritive spermatophores (Thornhill and Alcock, 1983; Boggs, 1990; Bissoondath and Wiklund, 1995). For example, the moth, *Utetheisa ornatrix* receives pyrrolizidine alkaloid, which she transmits to the eggs to protect them (Lamunyon, 1997). Nutritive spermatophore contents are common in the Lepidoptera, which are prominent in studies of female choice because of their frequent multiple mating and the baroque complexity of the female reproductive tract (Eberhard, 1985, 1996; Bissoondath and Wiklund, 1995; Morrow and Gage, 2000).

Sometimes females mate multiply because it is forced on them by males, something that is called convenience polyandry (Arnqvist, 1997; Rowe et al., 1994). In these cases mating is simply less costly than avoiding males that occupy an important resource for the females. In water striders males monopolize water surfaces where females lay their eggs. Though males may harass females into mating, the females have some control over which male actually fertilizes their eggs (Arnqvist and Danielsson, 1999; Pizzari and Birkhead, 2000). Mating may be the price female pseudoscorpions pay for access to harlequin beetle backs for transport, something which may explain their advanced post-copulatory mate choice talents (Zeh et al., 1998; Zeh and Zeh, 1992).

Multiple mating in the absence of force or material benefits may most commonly be the result of difficulties in identifying the highest quality mate. This would work only if post-copulatory choice mechanisms between males improved on the choice at first mating. It is now clear that genetic variation in males can be maintained even if males provide no other resources (see Jennions and Petrie, 2000, for an excellent review of this topic). In some birds there is clear evidence that females prefer higher quality mates, and that there is additive genetic variance for the chosen traits (Birkhead and Møller, 1992; Kempenaers et al., 1992, 1997; Pomiankowski and Møller, 1995; Johnson et al., 2000). If multiple mating is the result of difficulties in choosing the best mate, we would expect more multiple mating in species where males are harder to assess and choose as compared to males in leks where the best male can be identified more easily. How much choice a female actually has depends on the species and the type of lek, and may differ between insects and vertebrates (Bradbury, 1985).

A strategy of females that appears to be widespread is to mate rather unselectively with a first male to assure some mate at all, then to mate very selectively a second time, with the second male's sperm taking precedence (Walker, 1980; Thornhill and Alcock, 1983; Eberhard, 1996; Simmons and Siva-Jothy, 1998). If a female has chosen to mate a second time, whether it is sperm competition or female actions that causes that male's sperm to dominate, both are in her interests (Simmons and Siva-Jothy, 1998). Second male precedence in insects is associated with complexities in female sperm storage organs (Walker, 1980; Eberhard, 1996). Females also may mate more than once in case the first male was sterile (Krokene et al., 1998).

If females accidentally mate with males of other species, it will be to their advantage if the sperm that fertilizes their eggs is from a conspecific male. This has been shown in *Drosophila* to be the results of characteristics of seminal fluid interaction with the conspecific female's reproductive tract, and can override second male sperm precedence (Price, 1997). There can also be other finer level differences among males that might be assessed after mating. Multiple mating may reduce the risk of inbreeding (Stockley et al., 1993). Genetic compatibility may also vary among males, making different males optimum for different females (Wilson et al., 1997; Kempenaers et al., 1999; Newcomer et al., 1999, Zeh and Zeh, 1996, 1997). In sea urchins, sperm with alleles at the *bindin* locus that match those of the female are more successful (Palumbi, 1999).

If males and females pair up to rear babies, then a female may be unable to choose the best male as a social mate because he is already taken, but she could still copulate with him. Of course she would also copulate with her less attractive social mate if she expects him to help care for the young. This reasoning may explain the frequency of extra-pair copulations in passerine birds with pair bonds (Gowaty, 1996; Westneat et al., 1990, Birkhead and Møller, 1998).

Genetic diversity among progeny may be advantageous in highly variable environments, in circumstances where progeny compete especially intensely, the same circumstances where sex itself is advantageous (Williams, 1975; Ridley, 1993). Genetic diversity among progeny may also increase disease resistance (Schmid-Hempel, 1998; Baer and Schmid Hempel, 1999) and facilitate task differentiation in social insects (Fewell and Page, 1993, Page et al., 1995; Cole and Wiernasz, 1999).

Multiple mating does not necessarily imply multiple paternity in the young. If females have post-copulatory ways of discriminating, then some males may have a much greater chance of fertilizing eggs. Only the sperm depletion hypothesis and the genetic diversity hypothesis require that females use more than one male's sperm to obtain the advantage. We are gaining increasing understanding of the ways that females can select sperm from some matings over others (Eberhard, 1996). Often these involve multi-compartmented spermathecae (Eberhard, 1996 but see Ridley, 1989). These female choice factors can reduce the number of mates actually fathering brood in multiply mated species. Of course males will be selected to behave in ways that increase the probability that their sperm will actually fertilize eggs, but they are at a power disadvantage since they are often away from the scene by the time actual fertilization takes place. This conflict between the sexes may cause the observed rapidity of evolutionary change in genitalia shapes in species that mate multiply as compared to those with females that mate only once (Arnqvist, 1998).

The cost of mating should influence how readily a female will mate multiply (Thornhill and Alcock, 1983). Risks of mating include increased exposure to predators, waste of time, risks of injury by males, and disease transmission (Simmons and Siva-Jothy, 1998). In *Drosophila melanogaster* the products of male accessory glands have been shown to be toxic to females, reducing their longevity (Chapman et al., 1995). This cost of sexual selection to the females can be reduced if females and males are forced into monogamy and allowed to evolve over many generations (Holland and Rice, 1999). In spite of these costs, females in *D. melanogaster* regularly mate with multiple males in the wild (Imhof et al., 1998; Harshman and Clark, 1998). Females may be exposed to pathogens when they mate, and to more different ones when they mate with more males. Westneat and Rambo (2000) found that red-winged blackbird females were exposed to more kinds of bacteria in semen when they mated multiply. Males in the bean weevil damage the female's genital tract with hard spines, reducing female longevity (Crudgington and Siva-Jothy, 2000).

If the costs are low, then the advantages to multiple mating can be slight and various, which may explain why attempts to find a single cause for multiple mating have failed. If this is the case, then we would expect multiple mating to be as common and widespread as some authors claim (e.g. Eberhard, 1996). In fact, careful studies of the frequency of polyandry are rare (see Arnqvist, 1998 for an excellent example).

The impact of multiple mating on within-colony conflicts in social insects

Variation in queen number and mate number, and its impact on within-colony genetic conflicts has provided a rich arena for the investigation of kin selection (Hamilton 1964, 1972; Ratnieks, 1988; Bourke and Franks, 1995; Crozier and Pamilo, 1996; Queller and Strassmann, 1998). Multiple mating and multiple queens change the predictions for sex ratios, who should produce the males, queen succession, caste proportions, and within-colony kin preferences (e.g. Trivers and Hare, 1976; Starr, 1984; Page, 1986; Sundström, 1994; Keller and Reeve, 1994; Boomsma and Ratnieks, 1996; Peters et al., 1999). Perhaps the two most investigated areas are sex ratios and male production. Since males are haploid in the Hymenoptera and pass on identical sperm, sisters from a colony with a single, once-mated queen are related by 0.75. This means that on relatedness grounds workers will favor a 3:1 female-biased sex ratio in colonies with single once-mated queens, a prediction that provided the first robust evidence of worker control (Trivers and Hare, 1976). Worker sex ratio preferences will converge with those of the queen as mate number increases, or will lead to split sex ratios, with colonies headed by once-mated queens producing females and colonies with a multiply mated queen producing males (Boomsma and Grafen, 1990). Unmated workers as well as queens can produce males. This is another important area where the preferences of the workers and the queen change with mate number. Above a threshold of two mates in single queen colonies, workers prefer to rear the queen's sons rather than the sons of other workers (Starr, 1984; Ratnieks, 1988; Woyciechowski and Lomnicki, 1987). A queen can therefore obtain a more compliant workforce, at least with respect to male production and sex ratios, simply by mating multiply. Of course this argument depends on workers being able to determine how often their queen has mated, something that has been demonstrated for *Formica truncorum* (Sundström, 1993).

On the other hand, a reluctance to mate multiply will preserve elevated relatedness and facilitate the maintenance of sociality under more modest benefits relative to costs. However it is not obvious how this result could actively select for single mating by queens before a colony is formed. Of course it would be in the workers' interest to forbid any male from entering the colony and mating with their mother, something that might have forced mating into a narrow time window. Perhaps the finding (detailed below) that multiple mating is regular only in species with very large colonies and morphologically distinct workers is because these are the ones where workers have the fewest non-social options so that the mother's multiple mating does not lead to the loss of sociality.

Multiple queens are often posited as another way to arrive at genetically variable progeny, but the power situation there is very different since acceptance of multiple queens could be controlled by workers or queens (Boomsma and Ratnieks, 1996). Both workers and queens will end up with lower relatedness to brood if queens are added. For this reason, queens are more likely to favor multiple mating over multiple queens as a means of attaining genetic variation in the brood.

Hypotheses for multiple mating in social Hymenoptera

Of the seven hypotheses for multiple mating given in the introduction, three seem unlikely to apply to social insects: (1) material gain, (2) cost of avoiding males, (3) difficulties of access to the best possible male. Males do not provide nutritive mating plugs or gifts (Baer and Schmid-Hempel, 2000). They do not provide nests or territories or participate in the care of progeny or provide any other resource that would make mating for resources likely. A female must generally move her sting aside in order to copulate, reducing the probability of forced mating. Since there is no paternal care, females will not be forced to mate with a male to obtain his care for her young. Two other hypotheses seem unlikely because the requisite post-copulatory discrimination mechanisms required have not been demonstrated in social Hymenoptera. These two hypotheses are (1) difficulties in identifying the best male before mating with him, and (2) difficulties in identifying the most genetically compatible male. Even if either of these two did occur, they would not have a great impact on the social structure in the colony, since both result in the preponderance of the preferred male's sperm. Actual studies of multiple mating in social Hymenoptera show little evidence for preferential sperm usage or for clumped sperm though few studies have been done (Boomsma and Sundström, 1998; Haberl and Tautz, 1998).

The remaining hypotheses for multiple mating that might apply to social insects are that females mate multiply because of: (1) the need for more sperm, and (2) the advantages of a genetically diverse brood (Page and Metcalf, 1982; Cole, 1983; Crozier and Page, 1985; Ross, 1986; Ratnieks, 1990a; Keller and Reeve, 1994; Boomsma and Ratnieks, 1996; Sherman et al., 1988; Schmid-Hempel and Crozier, 1999). Social insects may have particular reasons both for more sperm and for a genetically diverse brood. They may have a particular need for more sperm since they mate only at one brief time, but then may live for many years, producing not only female reproductives with the stored sperm, but also thousands of workers (Cole, 1983). A genetically diverse brood can also be advantageous for special social insect reasons. The workers remain together in close proximity, which could facilitate disease transmission among them, so a genetically diverse brood could be more resistant to diseases (Schmid-Hempel and Crozier, 1999). Another advantage of a genetically diverse brood is that it could facilitate task specialization (Fewell and Page, 1993).

In addition to these two hypotheses there are two special social insect hypotheses. The first is based on the sex determining mechanism (Crozier and Page, 1985). An egg develops into a male if it is homozygous at the sex-determining locus. Normally this happens because the egg is haploid, but if it is homozygous at this locus, a diploid male will result, and they are usually sterile. Multiple mating might reduce the cost of diploid males if they could be identified and removed early in development (Crozier and Page, 1985; Ratnieks, 1990b; Pamilo et al., 1994). The second special social insect hypothesis concerns the reduction of queen/worker conflict. A queen might mate multiply to force workers into agreement with her regarding male production (Starr, 1984; Pamilo, 1991).

Data on mate number in social Hymenoptera

Boomsma and Ratnieks (1996) set new standards for evaluating mating frequency of social insect females. Earlier techniques for inferring multiple mating such as comparing male and female sperm counts, observations of apparent couplings, and genetic data uncontrolled for queen number are unreliable (Boomsma and Ratnieks, 1996). DNA microsatellite genotyping of female’s spermatheca contents are best for assessing mate number (Evans, 1993; Peters et al., 1995). Mate number of the queen can also be determined from the genotypes of brood if there is a single queen in the colony (Boomsma and Ratnieks, 1996). These techniques may not detect multiple mating in the cases where the sperm from only one male is retained. However when there is multiple mating, the sperm from more than one male are typically represented quite evenly in the brood (Boomsma and Sundström, 1998).

In Tables 1–7 effective paternity is given as estimated by the original author, as estimated by Boomsma and Ratnieks (1996), or as estimated from relatedness among daughters from a single queen using the relationship $M_e = 0.5/(r - 0.25)$ from Pamilo (1993). All estimates are based on genetic markers, either allozymes or DNA microsatellites.

Mate number in ants

Boomsma and Ratnieks (1996) did a careful survey of mate number in ant queens, concentrating on species with robust genetic data (Tables 1–2). They found single mating to predominate, with effective mate number of only 1.16 on average across the 19 species for which complete genetic data were available. Perhaps multiple mating is limited by male discrimination because of limits to their sperm stores since additional sperm are not produced after maturity (Hölldobler and Bartz, 1985). Against this general background of single mating, there are some species with queens that usually mate multiply. The ants are too large a group, and studies of mating are too few as of yet, to look for patterns across the entire group, but some specific groups have been closely studied.

The ponerine *Rhytidoponera* sp. 12 has reproductive females that typically mate only once (96 of 99 spermathecae examined, Tay and Crozier, 2000). This is in accord with the single mating found in all species with females that call in mates rather than joining mating swarms.

The fungus growing ants (Myrmicinae, Attini) have been studied in the most detail. Clearly, all 6 lower attines for

Table 1. Paternity in fungus growing ants (Attini, Myrmicinae)

Higher or lower attine	Species	Effective paternity	Sample size[a]	Reference
Lower	*Apterostigma collare*	1	10	Villesen et al., 1999
Lower	*Apterostigma mayri*	1.09	5	Murakami et al., 2000
Lower	*Cyphomyrmex costatus*	1.04	5	Murakami et al., 2000
Lower	*Cyphomyrmex longiscapus*	1	11	Villesen et al., 1999
Lower	*Cyphomyrmex rimosus*	1.14	5	Murakami et al., 2000
Lower	*Myrmicocrypta ednaella*	1 1.11	5 8	Villesen et al., 1999; Murakami et al., 2000
Higher	*Acromyrmex echinatior*	2.23	13	Bekkevold et al., 1999
Higher	*Acromyrmex octospinosus*	3.9 2.50	10 5	Boomsma et al., 1999 Murakami et al., 2000
Higher	*Atta sexdens*	2.3	6	Fjerdingstad and Boomsma, 2000
Higher	*Atta colombica*	1.87 3.13	6 11	Fjerdingstad et al., 1998; Murakami et al., 2000
Higher	*Sericomyrmex amabilis*	1.85	5	Murakami et al., 2000
Higher	*Trachymyrmex isthmicus*	0.94	5	Murakami et al., 2000

[a] Sample size is number of monogynous colonies evaluated or number of queens evaluated if queens are collected independently of their colonies and allowed to reproduce in the lab, or have their spermatheca evaluated.

which we have data have effective mate numbers of one, or very close to one (Table 1). By contrast, 5 of 6 higher attines have effective mate numbers above two (Table 1). Thus multiple mating is derived in the tribe Attini (Villesen et al., 1999; Murakami et al., 2000). Multiple mating in higher attines has been attributed to increased sperm stores (Fjerdingstad and Boomsma, 1997) in accord with Cole's hypothesis (Cole, 1983). However queens in *Atta colombica* and *Acromyrmex versicolor* have been shown to store only the number of sperm provided by a single male, which argues against this hypothesis (Fjerdingstad and Boomsma, 1997; Reichardt and Wheeler, 1996 but see Fjerdingstad and Boomsma, 1998). Multiple mating is also attributed to advantages of genetic diversity (Murakami et al., 2000, Villesen et al., 1999; Boomsma et al., 1999; Reichardt and Wheeler, 1996). Exactly why genetic diversity is advantageous in higher and not lower attines is not clear, but may be due to the complexity of maintaining fungus cultures, to the advantages of a diverse work force, or to enhanced disease resistance (Villesen et al., 1999; Reichardt and Wheeler, 1996; Boomsma et al., 1999). No support was found for the hypothesis that multiple mating reduces the burden imposed by diploid males (Boomsma et al., 1999).

The only other Myrmicine found to have high levels of multiple mating is *Pogonomyrmex occidentalis*, with an effective mate number of 6.76 (Cole and Wiernasz,1999, 2000a). If the colonies have multiple queens, something they could not entirely rule out, mate number may be lower (Fjerdingstad and Keller, 2000). Colonies with lower relatedness among workers, presumably due to multiple mating by the queen, had higher growth rates which the authors attributed to the advantages of genetic diversity (Cole and Wiernasz,

Table 2. Effective paternity in the non-fungus growers

Subfamily	Species	Effective paternity	Sample size[a]	Reference
Ponerinae	*Rhytidoponera* sp. 12	1.01	99	Tay and Crozier, 2000
Myrmicinae	*Aphaenogaster rudis*	<1.02[b]	47	Crozier, 1973, 1974
	Harpagoxenus sublaevis	<1.02[b]	49	Bourke et al., 1988
	Leptothorax nylanderi	1	12	Foitzik et al., 1997
	Leptothorax pergandei	1.04[b]	12	Heinze et al., 1995
	Myrmica rubra	1.21	22	Boomsma and Ratnieks, 1996; Seppä and Walin, 1996
	Myrmica ruginodis	1.07[b]	34	Seppä, 1994
	Myrmica sulcinodis	1.06	23	Pedersen and Boomsma, 1999
	Pogonomyrmex occidentalis	6.76	1492	Cole and Wiernasz, 2000
	Solenopsis geminata	<1.02[b]	30	Ross et al., 1987, 1988
	Solenopsis invicta	<1.01[b]	55	Ross and Fletcher, 1985
	Solenopsis richteri	<1.02[b]	58	Ross et al., 1987, 1988
Dolichoderinae	*Conomyrma insana*	<1.09[b]	34	Berkelhamer, 1984
Formicinae	*Colobopsis nipponicus*	1.03[b]	59	Hasegawa, 1994; in Boomsma and Ratnieks, 1996
	Formica aquilonia	1.48[b]	113	Pamilo, 1993
	Formica exsecta	1.35	56	Boomsma and Sundström, 1998
	Formica exsecta at Joskar	1.16[b]	19	Pamilo and Rosengren, 1983, 1984; Fortelius et al., 1987
	Formica fusca	1.11	21	Boomsma and Sundström, 1998
	Formica paralugubris	1.1	166	Chapuisat, 1998
	Formica pressilabris	1.12[b]	46	Pamilo, 1982; in Boomsma and Ratnieks, 1996
	Formica rufa	1.47	79	Boomsma and Sundström, 1998
	Formica sanguinea	1.31[b]	24	Pamilo, 1982; Pamilo and Varvio-Aho, 1979
	Formica transkaucasica	1.03[b]	60	Pamilo, 1982
	Formica truncorum	1.43[b]	116	Sundström, 1989, 1993
	Lasius niger at Amsterdam	1.46[b]	31	Van der Have et al., 1988
	Lasius niger several pops.	1.04–1.42	535	Boomsma and van der Have, 1998
	Lasius flavus	<1.2[b]	25	Boomsma et al., 1993
	Lasius neglectus	<1.36[b]	11	Boomsma et al., 1990

[a] Sample size is number of monogynous colonies evaluated or number of queens evaluated if queens are collected independently of their colonies and allowed to reproduce in the lab, or have their spermatheca evaluated.

[b] Effective paternity calculated by Boomsma and Ratnieks, 1996.

1999). However reproduction was not associated with colony size in this species (Cole and Wiernasz, 2000b)

Of the six species of *Myrmica* for which there are data, three (*M. tahoensis*, *M. punctiventris* and *M. lobicornis*) are singly mated and three are multiply mated, but maintain low effective mate numbers (*M. ruginodis*, *M. sulcinodis*, and *M. rubra*; Pedersen and Boomsma, 1999). Pedersen and Boomsma (1999) found that species with multiply-mated queens were more likely also to have multiple queens per colony, an association that goes directly against the genetic diversity hypothesis, but is consistent with the hypothesis that the elevated density of reproductives in a given area caused by restricted dispersal results in both multiple queens and multiple mating. All species of the ecologically very successful *Solenopsis* studied to date have exclusively singly-mated queens (Ross et al., 1987; Ross and Fletcher, 1985). Single mating is the rule for *Leptothorax* for which several species have been studied (Table 2; reviewed in Foitzik et al., 1997). The same is true for other Myrmicine species studied (see Table 1 and references therein).

Two genera of Formicine ants have been studied for mate number in some detail, *Lasius*, and *Formica* (Table 2). Queens of *Lasius* generally mate only once and have effective paternity values from 1.04 to 1.46 (Table 2; Boomsma and Ratnieks, 1996; Boomsma and Van der Have, 1998). When queens of *Lasius niger,* the most common ant in Europe, mate more than once it is in the second half of the mating flight (Boomsma and Van der Have, 1998). Bad weather shortens mating flights, reducing the chance of multiple mating (Boomsma and Leusink, 1981). Mating frequency by queens of *Lasius niger* varies among populations, and appears to be dependent on the number of males in the mating swarms (Boomsma and Van der Have, 1998). These results point to the importance of mating circumstances in determining mating frequency. There is no evidence for the diploid male hypothesis since diploid males are unknown in this species (Boomsma and Van der Have, 1998). There is also little evidence for paternity skew of either the first or second male (Boomsma and Van der Have, 1998).

Formica is the best-studied genus in the Formicinae (Table 2; Pamilo et al., 1994; Boomsma and Sundström, 1998). All species studied to date have effective mate numbers under 1.5, indicating a preponderance of singly-mated queens, but also appreciable frequencies of doubly and even triply-mated queens (Boomsma and Ratnieks, 1996; Boomsma and Sundström, 1998; Chapuisat, 1998). Workers in colonies with multiply-mated queens of *Formica truncorum* produce more males than colonies with singly-mated queens, in accord with worker control and split sex ratios (Sundström, 1994). This means that it would not be advantageous for a male to mate with an already-mated female since this might cause her to produce sons (who do not have fathers) and not daughters. Selection for such behavior in males might be difficult to achieve because any mistakes in assessment of the female's mating status would greatly reduce the male's fitness. If all queens mated multiply, selection for continent males would disappear. In accord with this hypothesis, Boomsma and Sundström (1998) found that the more frequent multiple mating was in a population, the more likely it was that sperm from both males were equally represented in the queen's progeny, though the effect was not large, and was dependent on one species. There is some evidence that diploid males are more frequent in *Formica* species with multiple mating, which would support this hypothesis for multiple mating, but other hypotheses can also explain this pattern (Pamilo et al., 1994). Chapuisat (1998) found no difference in mating frequency between queens of *Formica paralugubris* mating at safe locations near their natal nest, or mating after the more risky dispersal to distant fields. He argues that the occasional double mating in this species probably has no adaptive significance.

Data on the impact of the mating situation on multiple mating is hard to obtain in ants. They have two general kinds of mating systems: (1) male aggregations that females join to mate and (2) females calling males to them from the nest or close to the nest (Hölldobler and Bartz, 1985). Female calling species are generally singly-mated. At the aggregations males do not generally have territories. The males release pheromones to attract females to them. Sites for matings are often prominent and maintained from year to year (Woyciechowski, 1992). In *Pogonomyrmex* there was a tendency of larger males to pair with larger females, and smaller males to pair with smaller females (Davidson, 1982).

Mate number in social bees

The excitement about extreme polyandry in social insects comes partly from studies of honeybees because queens in all species of *Apis* studied to date mate multiply with effective mate numbers between 5.6 and 25.7 (Table 3; Estoup et al., 1994; Moritz et al., 1995, 1996; Oldroyd et al., 1995, 1997; Haberl and Tautz, 1999; Franck et al., 2000). Drones congregate at sites where the females go, and these sites may be the same for decades (Ruttner, 1985). At mating sites, drones always greatly outnumber queens. Their absolute density varies considerably among honeybee populations, a factor that has been considered to influence mate number in honeybee queens (Winston, 1987; Haberl and Tautz, 1998, 1999; Tarpy and Page, 2000). The queens mate in the air (reviewed in Ruttner, 1985, Winston, 1987, Seeley, 1985). They may take multiple mating flights, increasing the number of mates with each flight (Tarpy and Page, 2000). Males can mate only once, and leave a large mating plug that does not preclude

Table 3. Effective mate numbers in honeybees as estimated by Oldroyd et al., 1997

Species	Effective paternity	No. colonies	Original reference
Apis mellifera	12.4	5	Estoup et al., 1994
Apis florea	10.1	5	Palmer and Oldroyd, 2001
Apis dorsata	20.0	4	Moritz et al., 1995
	25.65	6	
Apis andreniformis	9.1	4	Oldroyd et al., 1997

future matings by the females (Ruttner, 1985). Even honeybees whose queens mate many times and produce many daughters do not retain more sperm than a single typical male can produce, arguing against the sperm depletion hypothesis (Crozier and Page, 1985).

Since queens often go on multiple mating flights (Tan et al., 1999), mating multiply is their choice, not inflicted upon them by the males. The costs of mating are notoriously difficult to quantify. For honeybees the risk of dying on a mating flight has been calculated at between 4.85% (Ratnieks, 1990a) and 6.25% (Tarpy and Page, 2000), or, alternatively, as 0.26% per minute of flight (Tarpy and Page, 2000).

The pet hypothesis for multiple mating in honeybees is the genetic variability hypothesis (Fuchs and Moritz, 1998). Colonies with greater levels of genetic variability have been shown to be more responsive to environmental variation relevant to foraging (Fewell and Page, 1993). Sperm is used randomly, just the sort of mix best for a genetic variability hypothesis (Haberl and Tautz, 1998). There has been no evidence for an association between mating frequency and colony size, success, or disease resistance (Neumann and Moritz, 2000).

Also in the Apidae are the stingless bees, the Meliponinae, with hundreds of species across the tropics. Like the honeybees, the stingless bees have single queen colonies (excepting only *Melipona bicolor),* hundreds to thousands of workers, and morphological differences between workers and queens, though these differences are slight in *Melipona* (Imperatriz-Fonseca et al., 1998; Michener, 2000). Stingless bee males hover around colony entrances where a virgin queen is likely to be available, and pursue her and mate with her as she leaves the colony (daSilva et al., 1972; Imperatriz-Fonseca et al., 1998). Stingless bee males leave a mating plug that may deter subsequent mating (Imperatriz-Fonseca and Zucchi, 1995). In *Tetragonisca angustula* two males were observed to lose their genitalia which might have meant both mated with the queen (Imperatriz-Fonseca et al., 1998).

Table 4. Mating frequency in stingless bees as assessed from genetic relatedness estimated from polymorphic microsatellite loci

Species	Effective paternity *	No. colonies	
Melipona quadrifasciata	0.86	4	Peters et al., 1999
Melipona panamica	0.96	9	Peters et al., 1999
Melipona beecheii	1.16	10	Paxton et al., 1999
Scaptotrigona postica	0.82	4	Peters et al., 1999
Scaptotrigona postica	1.61	7	Paxton, 2000
Scaptotrigona barrocoloradensis	0.85	4	Peters et al., 1999
Partamona near *cupira*	0.91	12	Peters et al., 1999
Schwarziana quadripunctata	0.93	4	Peters et al., 1999
Tetragona clavipes	1	7	Peters et al., 1999
Trigona fulviventris	1.16	7	Peters et al., 1999
Nannotrigona perilampoides	1.19	7	Peters et al., 1999
Lestrimellita limão	1.22	2	Peters et al., 1999
Paratrigona subnuda	1.35	5	Peters et al., 1999
Plebeia near *minima*	1.43	5	Peters et al., 1999

* Probably overestimates because this assumes all mismatched individuals are due to multiple mating, not to queen turnover or to drifting among colonies.

Stingless bees generally mate only once, according to DNA microsatellite data (Table 4; Peters et al., 1999), a result in accord with earlier behavioral, sperm count, and allozyme studies (Kerr et al., 1962; daSilva et al., 1972, Contel and Kerr, 1976; Machado et al., 1984). Peters et al. (1999) found all worker genotypes were consistent with a single once-mated queen in seven of the 13 species they investigated (Table 4). The very few anomalous genotypes in the remaining species are most likely to be due to queen turnover. *Melipona beecheii* and *Scaptotrigona postica* were found to have low levels of anomalous genotypes which would result in effective paternities of 1.1 and 1.4 respectively if they are due to multiple mating (Paxton, 2000; Paxton et al., 1999). They could also be explained by drifting workers from other colonies. Peters et al. (1999) did not find a single case of multiple mating in *S. postica* collected in the same part of Brazil. Effective mate number for stingless bees overall is 1.03. This is a large, successful group whose queens mate only once.

The stingless bees are an important challenge to the genetic diversity hypothesis since the subfamily contains species where it should be just as likely to apply as in the honeybees. Colonies can be just as large, are just as generally single queen, and have similar foods to which they recruit. Peters et al. (1999) found that mate number differences predict many of the differences between stingless bees and honey bees in worker-queen conflicts over male production and which queen leaves with the swarm.

Another important group in the Apidae is the bumble bees, which have single queens that independently begin nests in the spring, and have worker-queen caste differentiation (Table 5; Schmid-Hempel and Schmid-Hempel, 2000). Bumblebees mate on the substrate, and females appear to be able to avoid undesired matings by pushing the males away, keeping their genital opening closed, or even stinging the males to death (Duvoisin et al., 1999; Djegham et al., 1994). Mating takes longer in bumblebees as compared to honeybees, and the sticky mating plug may be harder to dislodge (Duvoisin et al., 1999). This mating plug has no nutritive value (Baer et al., 2000). A survey of 8 species across central Europe found multiple mating only in *B. hypnorum*, in agree-

Table 5. Multiple paternity in *Bombus* from Schmid-Hempel and Schmid-Hempel, 2000 (and data used therein from Estoup et al., 1995). All species have single queens

Species	Effective paternity	No. colonies
B. terrestris	1	17
B. lucorum	1	12
B. hypnorum	1.12	17
B. pratorum	1	5
B. lapidarius	1	11
B. sicheli	1	2
B. hortorum	1	5
B. pascuorum	1	6

ment with an earlier study, and the effective mate number in that species was only 1.12 (Table 5; Estoup et al., 1995; Schmid-Hempel and Schmid-Hempel, 2000). This is particularly interesting because colonies with forcibly multiply-mated queens have fewer parasites (Baer and Schmid-Hempel, 1999). Perhaps honeybees mate multiply because of fewer opportunities for female choice when mating in the air as compared to mating on the substrate the way bumblebees and stingless bees do.

Mate number in social wasps

In some respects wasps have been the most difficult group for assessment of multiple mating by queens because multiple queens or usurping queens make it easy to confuse multiple queens for multiple mates (as Metcalf and Whitt, 1977, probably did). Highly variable microsatellite loci, and genotyping sperm in female spermathecae has given us firm data for two of the three subfamilies: Polistinae and Vespinae (Tables 6 and 7). The Polistinae are exclusively singly-mated (Table 6). This includes wasps with very different life histories. *Polistes* colonies have single queens that begin nests alone and have no morphological difference between workers and queens. The neotropical Epiponini are swarm-founding, and colonies may be perennial but unlike bees or most ants, they have many queens during most of their colony cycle and slight or no caste differences (West Eberhard, 1978; Jeanne, 1991; Strassmann et al., 1991; Queller et al., 1993). Ropalidiini comprise species with small colonies like *Polistes* and large, many queen colonies like the Epiponini (Gadagkar, 1991).

The Vespinae differ from the Polistinae because they have queens that are much larger than workers (Wilson, 1971). Their colonies are annual and have single queens (Wilson, 1971). Multiple mating is common only in *Vespula,* which has effective mate numbers of 1.9 to 7.1, not in the other genera of vespine wasps (Table 7; Foster et al., 1999; 2001). In multiply mated females, sperm are mixed and used in equal proportions over time (Ross, 1986). Frequent multiple mating is derived in the Vespinae since the basal genera have mate numbers of 1 to 1.11 (Foster et al., 2001). However *Dolichovespula* has effective mate numbers of 1 to 1.35 and it is just as derived as *Vespula* (Foster et al., 2001).

Social wasps generally have a mating system similar to ants in that males congregate in certain places, but differ

Table 6. Evidence for single mating by females in Polistine wasps

Subfamily	Species	No. Effective paternity	No. queens assessed for mate number	Reference
Polistinae	*Polistes bellicosus*	1	63	Arévalo et al., 1998; Field et al., 1998
Polistinae	*Polistes annularis*	1.05	40	Peters et al., 1995
Polistinae	*Polistes carolina*	1	56	Seppa et al., submitted
Polistinae	*Polistes dorsalis*	1	6	Arévalo et al., 1998
Polistinae	*Polistes dominulus*	1	60	Queller et al., 2000; Zacchi, 1998
Polistinae	*Parachartergus colobopterus*	1	38	Goodnight et al., 1996
Polistinae	*Brachygastra mellifica*	1	43	Hastings et al., 1998
Polistinae	*Polybioides tabidus*	1	48	Henshaw et al., 2001

Table 7. Multiple paternity in Vespine wasps. All species have single queens

Higher or lower Vespine	Species	Effective paternity	No. colonies	Original reference (cited in Foster and Ratnieks, 2001 a)
Lower	*Vespa cabro*	1.11	14	Foster et al., 1999
Lower	*Dolichovespula media*	1.08	10	Foster et al., 2001
Lower	*Dolichovespula maculata*	1.00	10	Foster et al., 2001
Lower	*Dolichovespula arenaria*	1.09	20	Ratnieks and Boomsma, unpubl.
Lower	*Dolichovespula sylvestris*	1.15	10	Foster et al., 2001
Lower	*Dolichovespula norwegica*	1.08	10	Foster et al., 2001
Lower	*Dolichovespula saxonica*	1.35	10	Foster et al., 2001
Higher	*Vespula germanica*	2.35	55	Goodisman et al., unpubl.; Ross, 1985
Higher	*Vespula maculifrons*	7.14	30	Ross, 1985, 1986
Higher	*Vespula vulgaris*	1.90	17	Foster and Ratnieks, 2001b
Higher	*Vespula squamosa*	3.33	17	Ross, 1986

somewhat in male behavior at those sites (Ross and Matthews, 1991; Beani, 1996). In *Polistes,* males arrive at sites attractive to females such as treetops, telephone poles, towers or hibernacula, and there set up lek territories, fighting other males, defending the territories, and often smearing them with their gasters (reviewed in Beani, 1996). Females arrive later and choose their mates (Post, 1980; Post and Jeanne, 1983; Beani, 1996). Vespine males patrol vegetation, moving from place to place, with no clear territory (Post, 1980). Patrolling was also observed in males of neotropical swarm-founding wasps (Jeanne, 1991). These mating circumstances may facilitate female choice.

Overview of mating frequency of females in the social Hymenoptera

Of all the species of social Hymenoptera studied to date, only members of *Apis, Vespula, Pogonomyrmex,* and a monophyletic group of advanced fungus-growing ants have queens with effective mate numbers over two (Tables 1–7). All other groups of social Hymenoptera for which there is good evidence, from ants, to wasps, to bees, mate once, or if they mate more than once, do so seldom enough to keep effective mate numbers close to 1. For example, the highly successful, pantropical stingless bees have single once-mated queens even though they have large long-lived colonies with morphologically distinct workers that recruit to food sources as do honeybees. Another example comes from the polistine wasps where single mating holds across tribes with highly divergent colony longevities, colony sizes, and queen numbers.

Within many of these largely single-mating species are examples of individuals that have mated more than once. This means that there is not likely to be a general physical constraint against multiple mating. Therefore it would seem that if multiple mating were advantageous, it would be selected and would occur more commonly. Instead it seems that there is nothing intrinsic to sociality that strongly selects for multiple mating. If multiple mating was advantageous as a means for obtaining worker compliance in sex ratios and male production, then it would be expected to be much more common. If large, long-lived colonies were protected against diseases and parasites by the genetic diversity afforded by multiple mating, then we would expect it to occur in stingless bees, wasps, and ants that have colonies that can endure for years. If task specialization were much more effective with multiple genotypes, then we would expect it in the stingless bees and swarm-founding wasps where task specialization has been demonstrated. If queens living for many years were likely to run out of sperm, then we would expect them to mate multiply. That none of these patterns hold across a broad sampling of social Hymenoptera implies that multiple mating is not generally advantageous to social living.

Careful studies of multiple mating groups and the single-mating groups they derived from found no one hypothesis favoring multiple mating. Perhaps the only hypotheses with any support remaining are those based on the advantages of genetic diversity, though even here support is equivocal, not favoring either a disease resistance or a task specialization hypothesis consistently (Crozier and Page, 1985; Sherman et al., 1988; Keller and Reeve, 1994; Boomsma and Ratnieks, 1996; Baer and Schmid-Hempel, 1999; Schmid-Hempel and Crozier, 1999).

Perhaps there are differences between social Hymenoptera and non-social species that account for the rarity of multiple mating in social Hymenoptera. Social Hymenoptera do not get any material gains from mating more than once. They are not easily forced into mating, since they are particularly well-armed with stings, though the stingless bees bite instead of sting. The mating arenas may make it easier for social Hymenoptera to identify the best male before copulation. The lack of paternal care means they will not be constrained from mating with the best male they encounter. Perhaps what most sets social Hymenoptera apart is the generally narrow time window for mating. Queens mate at synchronized mating flights, just before hibernating, or during brief receptive periods before retreating to the protection of their nest (e.g. Ruttner, 1985; Beani, 1996). At these times multiple mating could occur with relatively little increased cost, but any cost to subsequent mating would be high since it would involve leaving the nest. Workers would be strongly selected not to let males enter the nest and mate with their queen because it would lower the workers' relatedness to brood.

The extreme multiple mating of honeybees stimulated a lot of thought about how sociality might favor multiple mating. But honeybees are a rare, almost singular exception to social Hymenoptera in general, mating many more times than any other group. In fact, sociality is usually expected to disfavor multiple mating because of the potentially large cost of reducing relatedness among brood. For a female in a primitively social species to choose to rear her mother's other progeny instead of her own progeny will require larger benefits relative to costs if the mother has mated multiply. This may mean that sociality was lost or never got started in groups where multiple mating was common. This would also explain the current scattered distribution of multiple mating in a few highly-social genera where workers have no non-social options.

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References

Andersson, 1994. *Sexual Selection.* Princeton University Press, Princeton, NJ. 599 pp.

Arévalo, E., J.E. Strassmann and D.C. Queller, 1998. Conflicts of interest in social insects: male production in two species of *Polistes. Evolution. 52:* 797–805.

Arnqvist, G., 1997. The evolution of water strider mating systems: causes and consequences of sexual conflicts. In: *The Evolution of Mating Systems in Insects and Arachnids* (J.C. Choe and B.J.

Crespi, eds.) Cambridge University Press, Cambridge. pp. 146–163.

Arnqvist, G., 1998. Comparative evidence for the evolution of genitalia by sexual selection. *Nature 393:* 784–786.

Arnqvist, G. and I. Danielsson, 1999. Postmating sexual selection: the effects of male body size and recovery period on paternity and egg production rate in a water strider. *Behav. Ecol. 10:* 358–365.

Arnqvist, G., M. Edvardsson, U. Friberg and T. Nilsson, 2000. Sexual conflict promotes speciation in insects. *Proc. Natl. Acad. Sci. 97:*10460–10464.

Arnqvist, G. and T. Nilsson, 2000. The evolution of polyandry: multiple mating and female fitness in insects. *Anim. Behav. 60:* 145–164.

Baer, B., R. Maile, P. Schmid-Hempel, E.D. Morgan and G.R. Jones, 2000. Chemistry of a mating plug in bumblebees. *J. Chem. Ecol. 26:* 1869–1875.

Baer, B. and P. Schmid-Hempel, 1999. Experimental variation in polyandry affects parasite loads and fitness in a bumblebee. *Nature 397:* 151–154.

Beani, L., 1996. Lek-like courtship in paper-wasps: 'a prolonged, delicate, and troublesome affair'. In: *Natural History and Evolution of Paper-wasps* (S. Turillazzi and M.J. West-Eberhard, eds.) Oxford University Press, Oxford. pp.113–125.

Bekkevold, D., J. Frydenberg and J.J. Boomsma, 1999. Multiple mating and facultative polygyny in the Panamanian leafcutter ant *Acromyrmex echinatior*. *Behav. Ecol. Sociobiol. 46:* 103–109.

Berkelhamer, R.C. 1984. An electrophoretic analysis of queen number in three species of Dolichoderine ants. *Insectes soc. 31:* 132–141.

Birkhead, T.R. and A.P. Møller, eds. 1998. *Sperm Competition and Sexual Selection.* Academic Press, San Diego, CA. 826 pp.

Birkhead, T.R. and A.P. Møller, 1992. *Sperm Competition in Birds.* Academic Press, New York. 282 pp.

Bissoondath, C.J. and C. Wiklund, 1995. Protein content of spermatophores in relation to monandry/polyandry in butterflies. *Behav. Ecol. Sociobiol. 37:* 365–371.

Boggs, C. 1990. A general model of the role of male-donated nutrients in female insects' reproduction. *Am. Nat. 136:* 598–617.

Boomsma, J.J., A.H. Brouwer and A.J. Van Loon, 1990. A new polygynous *Lasius* species (Hymenoptera: Formicidae) from Central Europe. II. Allozymatic confirmation of species status and social structure. *Insectes soc. 37:* 363–375.

Boomsma, J.J., E.J. Fjerdingstad and J. Frydenberg, 1999. Multiple paternity, relatedness and genetic diversity in *Acromyrmex* leafcutter ants. *Proc. R. Soc. Lond. 266:* 249–254.

Boomsma, J.J. and A. Grafen, 1990. Intraspecific variation in ant sex ratios and the Trivers-Hare hypothesis. *Evolution 44:* 1026–1034.

Boomsma, J.J. and A. Leusink, 1981. Weather conditions during nuptial flights of four European ant species. *Oecologia 50:* 236–241.

Boomsma, J.J. and F.L.W. Ratnieks, 1996. Paternity in social Hymenoptera. *Phil. Trans. R. Soc. Lond. 351:* 947–975.

Boomsma, J.J. and L. Sundström, 1998. Patterns of paternity skew in *Formica* ants. *Behav. Ecol. Sociobiol. 42:* 85–92.

Boomsma, J.J. and T.M. van der Have, 1998. Queen mating and paternity variation in the ant *Lasius niger*. *Molec. Ecol. 7:* 1709–1718.

Boomsma, J.J., P.J. Wright and A.H. Brouwer, 1993. Social structure in the ant *Lasius flavus:* multi-queen nests or multi-nest mounds? *Ecol. Entomol. 18:* 47–53.

Bourke A.F.G. and N.R. Franks, 1995. *Social Evolution in Ants.* Princeton University Press, Princeton, NJ. 529 pp.

Bourke, A.F.G., T.M. van der Have and N.R. Franks, 1988. Sex ratio determination and worker reproduction in the slave-making ant *Harpagoxenus sublaevis. Behav. Ecol. Sociobiol. 23:* 233–245.

Bradbury, J.W., 1985. Contrasts between insects and vertebrates in the evolution of male display, female choice, and lek mating. In: *Experimental Behavioral Ecology and Sociobiology* (B. Hölldobler and M. Lindauer, eds.) Sinauer Associates, Inc. Sunderland, New York. pp. 273–292.

Chapman, T., L.F. Liddle, J.M. Kalb, M.F. Wolfner and L. Partridge, 1995. Cost of mating in *Drosophila melanogaster* females is mediated by male accessory gland products. *Nature 373:* 241–244.

Chapuisat, M., 1998. Mating frequency of ant queens with alternative dispersal strategies, as revealed by microsatellite analysis of sperm. *Molec. Ecol. 7:* 1097–1105.

Choe, J.C. and B.J. Crespi, eds. 1997. *The Evolution of Mating Systems in Insects and Arachnids.* Cambridge University Press, Cambridge. 387 pp.

Cole, B.J., 1983. Multiple mating and the evolution of social behavior in the Hymenoptera. *Behav. Ecol. Sociobiol. 12:* 191–201.

Cole, B.J. and D.C. Wiernasz, 1999. The selective advantage of low relatedness. *Science 285*: 891–893.

Cole, B.J. and D.C. Wiernasz, 2000a. The nature of ant colony success: reply to Fjerdingstad and Keller. *Science 287:* 1363b.

Cole, B.J. and D.C. Wiernasz, 2000b. Colony size and reproduction in the western harvester ant, *Pogonomyrmex occidentalis. Insectes soc. 47:* 249–255.

Contel, E.P.B. and W.E. Kerr, 1976. Origin of males in *Melipona subnitida* estimated from data of an isozymic polymorphic system. *Genetica 46:* 271–277.

Crozier, R.H.,1973. Apparent differential selection at an isozyme locus between queens and workers of the ant *Aphaenogaster rudis. Genetics 73:* 33–318.

Crozier, R.H., 1974. Allozyme analysis of reproductive strategy in the ant *Aphaenogaster rudis. Isozyme Bull. 7:* 18.

Crozier, R.H. and R.E. Page, 1985. On being the right size: male contributions and multiple mating in social Hymenoptera. *Behav. Ecol. Sociobiol. 18:* 105–115.

Crozier, R.H. and P. Pamilo, 1996. *Evolution of Social Insect Colonies: Sex Allocation and Kin Selection.* Oxford University Press, Oxford. 306 pp.

Crudgington, H.S. and M. T. Siva-Jothy, 2000. Genital damage, kicking and early death. *Nature 407:* 855–856.

daSilva, D.L.N., R. Zucchi and W.E. Kerr, 1972. Biological and behavioural aspects of reproduction in some species of *Melipona* (Hymenoptera, Apidae, Meliponinae). *Anim. Behav. 20:* 123–132.

Davidson, D.W., 1982. Sexual selection in harvester ants (Hymenoptera: Formicidae: *Pogonomyrmex*). *Behav. Ecol. Sociobiol. 10:* 245–250.

Djegham, Y., J.C. Verhaege and P. Rasmont, 1994. Copulation of *Bombus terrestris* L. (Hymenoptera: Apidae) in captivity. *J. Apic. Res. 33:* 15–20.

Duvoisin, N., B. Baer and P. Schmid-Hempel, 1999. Sperm transfer and male competition in a bumblebee. *Anim. Behav. 58:* 743–749.

Eberhard, W.G.1985. *Sexual Selection and Animal Genitalia.* Harvard University Press, Cambridge, MA. 244 pp.

Eberhard, W.G. 1996. *Female Control: Sexual Selection by Cryptic Female Choice.* Princeton University Press, Princeton, NJ, 501 pp.

Estoup, A., A. Scholl, A. Pouvreau and M. Solignac, 1995. Monoandry and polyandry in bumble bees (Hymenoptera; Bombinae) as evidenced by highly variable microsatellites. *Molec. Ecol. 4:* 89–93.

Estoup, A., M. Solignac, M. Harry and J.M. Cornuet, 1993. Characterization of (GT)n and (CT)n microsatellites in two insect species: *Apis mellifera* and *Bombus terrestris*. *Nucl. Acids Res. 21:* 1427–1431.

Estoup, A., M. Solignac and J.M. Cornuet, 1994. Precise assessment of the number of patrilines and of genetic relatedness in honeybee colonies. *Proc. R. Soc. Lond. 258:* 1–7.

Evans, J.D. 1993. Parentage analyses in ant colonies using simple sequence repeat loci. *Molec. Ecol. 2:* 393–397.

Fewell, J.H. and R. E. Page, 1993. Genotypic variation in foraging responses to environmental stimuli by honey bees, *Apis mellifera*. *Experientia. 19:* 1106–1112.

Field, J., C.R. Solís, D. C. Queller and J.E. Strassmann, 1998. Social and gentic structure of paper wasp cofoundress associations: tests of reproductive skew models. *Am. Nat. 151:* 545–563.

Fjerdingstad, E.J. and J.J. Boomsma, 1997. Variation in size and sperm content of sexuals in the leafcutter ant, *Atta colombica. Insectes soc. 44:* 209–218.

Fjerdingstad, E.J. and J.J. Boomsma, 1998. Multiple mating increases the sperm stores of *Atta colombica* leafcutter ant queens. *Behav. Ecol. Sociobiol. 42:* 257–261.

Fjerdingstad E.J. and J.J. Boomsma, 2000. Queen mating frequency and relatedness in young *Atta sexdens* colonies. *Insectes Sociaux. 47:* 354–356.

Fjerdingstad, E.J., J.J. Boomsma and P. A. Thorén, 1998. Multiple paternity in the leafcutter ant *Atta colombica* – a microsatellite DNA study. *Heredity 80:* 118–126.

Fjerdingstad, E.J. and L. Keller, 2000. The nature of ant colony success. *Science 287*: 1363b.

Foitzik, S., M. Haberl, J. Gadau and J. Heinze, 1997. Mating frequency of *Leptothorax nylanderi* ant queens determined by microsatellite analysis. *Insectes soc. 44:* 219–227.

Fortelius, W., P. Pamilo, R. Rosengren and L. Sundström, 1987. Male size dimorphism and alternative reproductive tactics in *Formica exsecta* ants (Hymenoptera: Formicidae). *Ann. Zool. Fenn. 24:* 45–54.

Foster, K.R., P. Seppä, F. L. W. Ratnieks and P. A. Thorén, 1999. Low paternity in the hornet *Vespa crabro* indicates that multiple mating by queens is derived in vespine wasps. *Behav. Ecol. Sociobiol. 46:* 252–257.

Foster, K.R. and F.L.W. Ratnieks, 2001. Paternity, reproduction and conflict in vespine wasps: a model system for testing kin selection predictions. *Behav. Ecol. Sociobiol.* In press.

Franck, P., N. Koeniger, G. Lahner, R.M. Crewe and M. Solignac, 2000. Evolution of extreme polyandry: an estimate of mating frequency in two African honeybee subspecies, *Apis mellifera monticola* and *A.m. scutellata. Insectes soc. 47:* 364–370.

Fuchs, S. and R.F.A. Moritz, 1998. Evolution of extreme polyandry in the honeybee *Apis mellifera* L. *Behav. Ecol. Sociobiol. 9:* 269–275.

Gadagkar, R., 1991. *Belonogaster, Mischocyttarus, Parapolybia* and independent-founding *Ropalidia*. In: *The Social Biology of Wasps* (K.G. Ross and R.W. Matthews, eds.) Comstock Publishing Associates, Ithaca. pp. 149–190.

Gagneux, P., C. Boesch and D. S. Woodruff, 1999. Female reproductive strategies, paternity, and community structure in wild West African chimpanzees. *Anim. Behav. 57:* 19–32.

Goodnight, K., J.E. Strassmann, C. J. Klingler and D. C. Queller, 1996. Single mating and its implications for kinship structure in a multiple-queen wasp, *Parachartergus colobopterus*. *Ethol. Ecol. Evol. 8:* 191–198.

Gowaty, P.A., 1994. Architects of sperm competition. *Trends Ecol. Evol. 9:* 160–161.

Gowaty, P.A., 1996. Battles of the sexes and origins of monogamy. In: *Partnerships in Birds: The Study of Monogamy* (J.M. Black, ed.) Oxford University Press, Oxford. pp. 21–52.

Haberl, M. and D. Tautz, 1999. Paternity and maternity frequencies in *Apis mellifera sicula*. *Insectes soc. 46:* 137–145.

Haberl, M. and D. Tautz, 1998. Sperm usage in honey bees. *Behav. Ecol. Sociobiol. 42:* 247–255.

Hamilton, W.D., 1972. Altruism and related phenomena, mainly in social insects. *Ann. Rev. Ecol. Sys. 3:* 193–232.

Hamilton, W.D., 1964. The genetical evolution of social behavior. *J. Theor. Biol. 7:* 1–52.

Harshman, L.G. and A.G. Clark, 1998. Inference of sperm competition from broods of field-caught *Drosophila*. *Evolution. 52:* 1334–1341.

Hasegawa, E. 1994. Sex allocation in the ant *Colobopsis nipponicus* (Wheeler). I. Population sex ratio. *Evolution 48:* 1121–1129.

Hastings, M.D., D.C. Queller, F. Eischen and J.E. Strassmann, 1998. Kin selection, relatedness, and worker control of reproduction in a large-colony epiponine wasp, *Brachygastra mellifica*. *Behav. Ecol. 9:* 573–581.

Heinze, J., B. Hölldobler and S. Trenkle, 1995. Reproductive behavior in the ant *Leptothorax (Dichothorax) pergandei. Insectes soc. 42:* 309–315.

Henshaw, M.T., J.E. Strassmann and D.C. Queller, 2000. The independent origin of a queen number bottleneck that promotes cooperation in the African swarm-founding wasp, *Polybioides tabidus*. *Behav. Ecol. Sociobiol. 48:* 478–483.

Holland, B. and W.R. Rice, 1999. Experimental removal of sexual selection reverses intersexual antagonistic coevolution and removes a reproductive load. *Proc. Natl. Acad. Sci. 96:* 5083–5088.

Hölldobler, B. and S.H. Bartz, 1985. Sociobiology of reproduction in ants. In: *Experimental Behavioral Ecology and Sociobiology* (B. Hölldobler and M. Lindauer, eds.) Sinauer Associates, Inc. Sunderland, New York. pp. 237–258.

Imhof, M., B. Harr, G. Brem and C. Schlötterer, 1998. Multiple mating in wild *Drosophila melanogaster* revisited by microsatellite analysis. *Molec. Ecol. 7:* 915–917.

Imperatriz-Fonseca, V.L., E.T. Matos, F. Ferreira and H. H. W. Velthuis, 1998. A case of multiple mating in stingless bees (Meliponinae). *Insectes soc. 45:* 231–233.

Imperatriz-Fonseca, V.L. and R. Zucchi, 1995. Virgin queens in stingless (Apidae, Meliponinae) colonies: a review. *Apidologie 26:* 231–244.

Jeanne, R.L., 1991. The swarm-founding Polistinae. In: *The Social Biology of Wasps* (K.G. Ross and R.W. Matthews, eds.) Comstock Publishing Associates, Ithaca. pp 191–231.

Jennions, M.D. and M. Petrie, 2000. Why do females mate multiply? A review of the genetic benefits. *Biol. Rev. 75:* 21–64.

Johnson, K., E. DuVal, M. Kielt and C. Hughes, 2000. Male mating strategies and the mating system of great-tailed grackles. *Behav. Ecol. 11:* 132–141.

Keller, L. and H.K. Reeve, 1994. Genetic variability, queen number, and polyandry in social Hymenoptera. *Evolution 48:* 694–704.

Kempenaers, B., B. Congdon, P. Boag and R.J. Robertson, 1999. Extrapair paternity and egg hatchability in tree swallows: evidence for the genetic compatibility hypothesis? *Behav. Ecol. 10:* 304–311.

Kempenaers, B., G.R. Verheyen and A.A. Dhondt, 1997. Extrapair paternity in the blue tit (*Parus caeruleus*): female choice, male characteristics, and offspring quality. *Behav. Ecol. 8:* 481–492.

Kempenaers, B., G.R. Verheyen, M. Van den Broeck, T. Burke, C. Van Broeckhoven and A. A. Dhondt, 1992. Extra-pair paternity results from female preference for high-quality males in the blue tit. *Nature 357:* 494–496.

Kerr, W.E., R. Zucchi, J.T. Nakadaira and J.E. Butolo, 1962. Reproduction in the social bees. *J. N.Y. Entomol. Soc. 70:* 265–276.

Krokene, C., K. Rigstad, M. Dale and J.T. Lifjeld, 1998. The function of extrapair paternity in blue tits and great tits: good genes or fertility insurance? *Behav. Ecol. 9:* 649–656.

LaMunyon, C.W., 1997. Increased fecundity, as a function of multiple mating, in an arctiid moth, *Utetheisa ornatrix*. *Ecol. Entomol. 22:* 69–73.

Machado, M.F.P., E.P.B. Contel and W.E. Kerr, 1984. Proportion of males sons-of-the-queen and sons-of-workers in *Plebeia droryana* (Hymenoptera, Apidae) estimated from data of an MDH isozymic polymorphic system. *Genetica 65:* 193–198.

Metcalf, R.A. and G.S. Whitt, 1977. Intra-nest relatedness in the social wasp *Polistes metricus*. A genetic analysis. *Behav. Ecol. Sociobiol. 2:* 339–351.

Michener, C.D. 2000. *The Bees of the World.* Johns Hopkins University Press, Baltimore, MD. 913 pp.

Moritz, R.F.A., P. Kryger and M. Allsopp, 1996. Competition for royalty in bees. *Nature 384:* 31.

Moritz, R.F.A., P. Kryger, G. Koeniger, N. Koeniger, A. Estoup and S. Tingek, 1995. High degree of polyandry in *Apis dorsata* queens detected by DNA microsatellite variability. *Behav. Ecol. Sociobiol. 37:* 357–363.

Morrow, E.H. and M.J.G. Gage, 2000. The evolution of sperm length in moths. *Proc. R. Soc. Lond. 267:* 307–313.

Mueller, U.G., S. Rehner and T.R. Schultz, 1998. The evolution of agriculture in ants. *Science. 281:* 2034–2038.

Murakami, T., S. Higashi and D. Windsor, 2000. Mating frequency, colony size, polyethism and sex ratio in fungus-growing ants (Attini). *Behav. Ecol. Sociobiol. 48*: 276–284.

Neumann, P. and R.F.A. Moritz, 2000. Testing genetic variance hypotheses for the evolution of polyandry in the honeybee (*Apis mellifera* L.) *Insectes soc. 47:* 271–279.

Newcomer, S.D., J.A. Zeh and D.W. Zeh, 1999. Genetic benefits enhance the reproductive success of polyandrous females. *Proc. Natl. Acad. Sci. 96:* 10236–10241.

Oldroyd, B.P., M.J. Clifton, S. Wongsiri, T.E. Rinderer, H.A. Sylvester and R.H. Crozier, 1997. Polyandry in the genus *Apis*, particularly *Apis andreniformis*. *Behav. Ecol. Sociobiol. 40:* 17–26.

Oldroyd, B.P., A.J. Smolenski, J.-M. Cornuet, S. Wongsiri, A. Estoup, T. Rinderer and R.H. Crozier, 1995. Levels of polyandry and intracolonial genetic relationships in *Apis florea*. *Behav. Ecol. Sociobiol. 37:* 329–335.

Page, R.E. 1986. Sperm utilization in social insects. *Ann. Rev. Entomol. 31*: 297–320.

Page, R.E. and R.A. Metcalf, 1982. Multiple mating, sperm utilization and social evolution. *Amer. Natur. 119*: 263–281.

Page, R.E., G.E. Robinson, M. K. Fondrk and M.E. Nasr, 1995. Effects of worker genotype diversity on honey bee colony development and behavior (*Apis mellifera* L.). *Behav. Ecol. Sociobiol. 36:* 387– 396.

Palmer K.A. and B.P. Oldroyd, 2001. Mating frequency in *Apis florea* revisited (Hymenoptera, Apidae). *Insectes soc. 48:* 40–43.

Palumbi, S.R., 1999. All males are not created equal: Fertility differences depend on gamete recognition polymorphisms in sea urchins. *Proc. Natl Acad. Sci. 96:* 12632–12637.

Pamilo, P. 1982. Multiple mating in *Formica* ants. *Hereditas 97: 37–45.*

Pamilo, P. 1991. Evolution of colony characteristics in social insects. II. Number of reproductive individuals. *Am. Nat. 138:* 412–433.

Pamilo, P. 1993. Polyandry and allele frequency differences between the sexes in the ant *Formica aquilonia. Heredity 70:* 472–480.

Pamilo, P. and R. Rosengren, 1983. Sex ratio strategies in *Formica* ants. *Oikos 40: 24–35.*

Pamilo, P. and R. Rosengren, 1984. Evolution of nesting strategies of ants: Genetic evidence from different population types of *Formica* ants. *Biol. J. Linn. Soc. 21:* 331–348.

Pamilo, P., L. Sundström, W. Fortelius and R. Rosengren, 1994. Diploid males and colony-level selection in *Formica* ants. *Ethol. Ecol. Evol. 6:* 221–235.

Pamilo, P. and S. Varvio-Aho, 1979. Genetic structure of nests in the ant *Formica sanguinea. Behav. Ecol. Sociobiol. 6:* 91–98.

Paxton, R.J., 2000. Genetic structure of colonies and a male aggregation in the stingless bee *Scaptotrigona postica*, as revealed by microsatellite analysis. *Insectes soc. 47:* 63–69.

Paxton, R.J., N. Weißschuh, W. Engels, K. Hartfelder and J.J.G. Quezada-Euán, 1999. Not only single mating in stingless bees. *Naturwissenschaften 86:* 143–146.

Pedersen, J.S. and J.J. Boomsma, 1999. Multiple paternity in social Hymenoptera: estimating the effective mate number in single-double mating populations. *Molec. Ecol. 8:* 577–587.

Pedersen, J.S. and J.J. Boomsma, 1999. Positive association of queen number and queen-mating frequency in *Myrmica* ants: a challenge to the genetic-variability hypotheses. *Behav. Ecol. Sociobiol. 45:* 185–193.

Peters, J.M., D.C. Queller, V.L. Imperatriz-Fonseca, D.W. Roubik and J. E. Strassmann, 1999. Mate number, kin selection, and social conflicts in stingless bees and honeybees. *Proc. R. Soc. Lond. 266:* 379–384.

Peters, J.M., D.C. Queller, J.E. Strassmann and C.R. Solís, 1995. Maternity assignment and queen replacement in a social wasp. *Proc. R. Soc. Lond. 260:* 7–12.

Pizzari, T. and T.R. Birkhead, 2000. Female feral fowl eject sperm of subdominant males. *Nature 405:* 787–789.

Pomiankowski, A. and A.P. Møller, 1995. A resolution of the lek paradox. *Proc. R. Soc. Lond. 260:* 21–29.

Post, D.C., 1980. Observations on male behavior of the Eastern yellowjacket, *Vespula maculifrons* (Hymenoptera: Vespidae). *Ent. News. 91:* 113–116.

Post, D.C. and R.L. Jeanne, 1983. Male reproductive behavior of the social wasp *Polistes fuscatus* (Hymenoptera: Vespidae). *Z. Tierpsychol. 62:* 157–171.

Price, C.S.C., 1997. Conspecific sperm precedence in *Drosophila*. *Nature. 388:* 663–666.

Queller, D.C., 1993. Worker control of sex ratios and selection for extreme multiple mating by queens. *Am. Nat. 142:* 346–351.

Queller, D.C. and J.E. Strassmann, 1998. Kin selection and social insects. *Bioscience 48:* 165–175.

Queller, D.C., J.E. Strassmann, C.R. Solís, C.R. Hughes and D.M. DeLoach, 1993. A selfish strategy of social insect workers that promotes social cohesion. *Nature 365:* 639–641.

Queller, D.C., F. Zacchi, R. Cervo, S. Turillazzi, M.T. Henshaw, L.A. Santorelli and J.E. Strassmann, 2000. Unrelated helpers in a social insect. *Nature 405:* 784–787.

Ratnieks, F.L.W., 1990a. Assessment of queen mating frequency by workers in social Hymenoptera. *J. Theor. Biol. 142:* 87–93.

Ratnieks, F.L.W., 1990b. The evolution of polyandry by queens in social Hymenoptera: the significance of the timing of removal of diploid males. *Behav. Ecol. Sociobiol. 26:* 343–348.

Ratnieks, F.L.W., 1988. Reproductive harmony via mutual policing by workers in eusocial Hymenoptera. *Am. Nat. 132:* 217–236.

Reichardt, A.K. and D.E. Wheeler, 1996. Multiple mating in the ant *Acromyrmex versicolor*: a case of female control. *Behav. Ecol. Sociobiol. 28:* 219–225.

Ridley, M., 1989. The incidence of sperm displacement in insects: four conjectures, one corroboration. *Biol. J. Linn. Soc. 38:* 349–367.

Ridley, M., 1993. Clutch size and mating frequency in parasitic Hymenoptera. *Am. Nat. 142:* 893–910.

Ross, K.G., 1986. Kin selection and the problem of sperm utilization in social insects. *Nature 323:* 798–800.

Ross, K.G. and D.J.C. Fletcher, 1985. Comparative study of genetic and social structure in two forms of the fire ant, *Solenopsis invicta. Behav. Ecol. Sociobiol. 17:* 349–356.

Ross, K.G. and R.W. Matthews, 1991. *The Social Biology of Wasps.* Comstock Publishing Associates, Ithaca, NY. 678 pp.

Ross, K.G., E.L. Vargo and D.J.C. Fletcher, 1987. Comparative biochemical genetics of three fire ant species in North America, with special reference to the two social forms of *Solenopsis invicta* (Hymenoptera: Formicidae). *Evolution 41:* 979–990.

Ross, K.G., E.L. Vargo and D.J.C. Fletcher 1988. Colony genetic structure and queen mating frequency in fire ants of the subgenus *Solenopsis* (Hymenoptera: Formicidae). *Biol. J. Linn. Soc. 34:* 105–117.

Rowe, L., G. Arnqvist, A. Sih and J.J. Krupa, 1994. Sexual conflict and the evolutionary ecology of mating patterns: water striders as a model system. *Trends Ecol. Evol. 9:* 289–293.

Ruttner, F., 1985. Reproductive behavior in honeybees. In: *Experimental Behavioral Ecology and Sociobiology* (B. Hölldobler and M. Lindauer, eds.) Sinauer Associates, Inc. Sunderland, New York. pp. 225–236.

Schmid-Hempel, P. 1998. *Parasites in Social Insects.* Princeton University Press, Princeton, NJ. 409 pp.

Schmid-Hempel, P. and R.H. Crozier, 1999. Polyandry versus polygyny versus parasites. *Phil. Trans. R. Soc. Lond. 354:* 507–515.

Schmid-Hempel, R. and P. Schmid-Hempel, 2000. Female mating frequencies in *Bombus* spp. from Central Europe. *Insectes soc. 47:* 36–41.

Seeley, T., 1985. *Honeybee Ecology: A Study of Adaptation in Social Life.* Princeton University Press, Princeton, NJ. 201 pp.

Seppä, P., 1994. Sociogenetic organization of the ants *Myrmica ruginodis* and *Myrmica lobicornis:* Number, relatedness and longevity of reproducing individuals. *J. Evol. Biol. 7: 71–95.*

Seppä, P., D.C. Queller and J.E. Strassmann, Submitted. Social conventions, competition, contracts and skew in young colonies of the social wasp, *Polistes carolina*.

Seppä, P. and L. Walin, 1996. Sociogenetic organization of the red ant *Myrmica rubra*. *Behav. Ecol. Sociobiol. 38:* 207–217.

Sherman, P. W., T.D. Seeley and H.K. Reeve, 1988. Parasites, pathogens, and polyandry in social Hymenoptera. *Am. Nat. 131:* 602–610.

Simmons, L.W. and M.T. Siva-Jothy, 1998. Sperm competition in insects: mechanisms and the potential for selection. In: *Sperm Competition and Sexual Selection* (T.R. Birkhead and A.P. Møller, eds.) Academic Press, San Diego. pp. 341–434.

Starr, C. K., 1984. Sperm competition, kinship, and sociality in the Aculeate Hymenoptera. In: *Sperm Competition and the Evolution of Animal Mating Systems* (R.L. Smith, ed.) Academic Press, Inc., Orlando, FL. pp. 427–464.

Stockley, P., J.B. Searle, D.W. Macdonald and C.S. Jones, 1993. Female multiple mating behavior in the common shrew as a strategy to reduce inbreeding. *Proc. R. Soc. Lond. 254:* 173–179.

Strassmann, J.E., D.C. Queller, C.R., Solís and C.R. Hughes, 1991. Relatedness and queen number in the neotropical wasp, *Parachartergus colobopterus*. *Anim. Behav. 42:* 461–470.

Sundström, L. 1989. Genetic relatedness and population structure in *Formica truncorum* Fabr. (Hymenoptera: Formicidae). *Acta Coll. Insect. Soc. 5:* 93–100.

Sundström, L. 1993. Genetic population structure and sociogenetic organisation in *Formica truncorum* (Hymenoptera: Formicidae). *Behav. Ecol. Sociobiol. 33:* 345–354.

Sundström, L., 1994. Sex ratio bias, relatedness asymmetry and queen mating frequency in ants. *Nature 367:* 266–268.

Tan, N.Q., M. Mardan, P.H. Thai and P.H. Chinh, 1999. Observations on multiple mating flights of *Apis dorsata* queens. *Apidologie 30:* 339–346.

Tarpy, D.R. and R.E. Page, 2000. No behavioral control over mating frequencies in queen honey bees (*Apis mellifera* L.): Implications for the evolution of extreme polyandry. *Am. Nat. 155:* 820–827.

Tay, W.T. and R.H. Crozier, 2000. Microsatellite analysis of gamergate relatedness of the queenless ponerine ant *Rhytidoponera* sp 12. *Insectes soc. 47:* 188–192.

Thornhill, R. and J. Alcock, 1983. *The Evolution of Mating Systems.* Harvard University Press, Cambridge, MA. 547 pp.

Trivers, R. L. and H. Hare, 1976. Haplodiploidy and the evolution of social insects. *Science 191:* 249–263.

Van der Have, J.J. Boomsma and S. B. Menken, 1988. Sex investment ratios and relatedness in the monogynous ant *Lasius niger* (L.). *Evolution* 42: 160–172.

Villesen, P., P.J. Gertsch, J. Frydenberg, U.G. Mueller and J.J. Boomsma, 1999. Evolutionary transition from single to multiple mating in fungus-growing ants. *Molec. Ecol. 8:* 1819–1825.

Walker, W.F., 1980. Sperm utilization strategies in nonsocial insects. *Am. Nat. 115:* 780–799.

West-Eberhard, M.J., 1978. Temporary queens in *Metapolybia* wasps: nonreproductive helpers without altruism? *Science 200:* 441–443.

Westneat, D.F. and T.B. Rambo, 2000. Copulation exposes Red-Winged Blackbirds to bacteria in male semen. *J. Avian Biol. 31:* 1–7.

Westneat, D.F., P.W. Sherman and M.L. Morton, 1990. The ecology and evolution of extra-pair copulations in birds. *Current Ornithology. 7:* 331–369.

Williams, G.C., 1975. *Sex and Evolution.* Princeton University Press, Princeton NJ. 200 pp.

Wilson, E.O., 1971. *The Insect Societies.* Harvard University Press. Cambridge MA. 548 pp.

Wilson, N., S.C. Tubman, P. E. Eady and Robertson, G.W., 1997. Female genotype affects male success in sperm competition. *Proc. R. Soc. Lond. 264:* 1491–1495.

Winston, M., 1987. *The Biology of the Honeybee.* Harvard University Press, Cambridge, MA. 281 pp.

Woyciechowski, M., 1992. Nuptial flights of ants (Hymenoptera, Formicidae) and their aerial aggregations. In: *Biology and Evolution of Social Insects* (J. Billen, ed.) Leuven University Press, Leuven, Belgium. 41–45.

Woyciechowski, M. and A. Lomnicki, 1987. Multiple mating of queens and the sterility of workers among eusocial Hymenoptera. *J. Theor. Biol. 128:* 317–327.

Zacchi, F., 1998. Genetic structure of *Polistes dominulus* foundress associations. Ph.D. Dissertation, Rice University, Houston, TX. 251 pp.

Zeh, D.W. and J.A. Zeh, 1992. Dispersal-generated sexual selection in a beetle-riding pseudoscorpion. *Behav. Ecol. Sociobiol. 30:* 135–142.

Zeh, J.A., S.D. Newcomer and D.W. Zeh, 1998. Polyandrous females discriminate against previous mates. *Proc. Natl Acad. Sci. 95:* 13732–13736.

Zeh, J.A. and D.W. Zeh., 1996. The evolution of polyandry. I. Intragenomic conflict and genetic incompatibility. *Proc. R. Soc. Lond. 263:* 1711–1717.

Zeh, J.A. and D.W. Zeh, 1997. The evolution of polyandry. II. Postcopulatory defences against genetic incompatibility. *Proc. R. Soc. Lond. 264:* 69–75.

Zeh, J.A. and D.W. Zeh, 1994. Last-male sperm precedence breaks down when females mate with three males. *Proc. R. Soc. Lond. 257:* 287–292.

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