Review article

Male mating behaviour and mating systems of bees: an overview[1]

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Abstract – Considerable interspecific diversity exists among bees in the rendezvous sites where males search for females and in the behaviours employed by males in their efforts to secure matings. I present an evolutionary framework in which to interpret this variation, and highlight the importance for the framework of (i) the distribution of receptive (typically immediate post-emergence) females, which ordinarily translates into the distribution of nests, and (ii) the density of competing males. Other than the highly polyandrous honey bees (*Apis*), most female bees are thought to be monandrous, though genetic data with which to support this view are generally lacking. Given the opportunity, male bees are typically polygamous. I highlight intraspecific diversity in rendezvous site, male behaviour and mating system, which is in part predicted from the conceptual framework. Finally, I suggest that inbreeding may be far more widespread among bees than has hitherto been considered the case.

Apoidea / rendezvous site / scramble competition / territoriality / inbreeding

1. INTRODUCTION

To the field biologist, the males of many insect species are often more apparent than females because of their ornate armature and fastidious courtship displays, as the calling of male grasshoppers (Orthoptera) and cicadas (Hemiptera) testifies (Thornhill and Alcock, 1983). Similarly for many bee species, males are the more readily observable sex as they search for receptive females at flowers, across hedgerows and trees, or as they course over a nesting aggregation. The literary caricature of the idling drone is probably far from the truth. A more appropriate view is that of the frenetic male in desperate search of an elusive, receptive female. There is consequently a plethora of reports, old and new, on male bees and their mate seeking behaviour (e.g. Haas, 1960; Peakall and Schiestl, 2004), though most studies are phenomenological. That is, they describe the encounter or *rendezvous site* at which males search for receptive females and where mating is thought to occur. Darwin (1886 in Alford, 1975) himself wrote at length on the flight routes of bumble bee (*Bombus* spp.) males in his own garden.

These studies have demonstrated the wide range of rendezvous sites and behaviours employed by male bees to secure mates (reviewed in Barrows, 1976; Alcock et al., 1978; Eickwort and Ginsberg, 1980; Ayasse et al., 2001; Willmer and Stone, 2005). The relative abundance and ease of observation of many male bees has also lent them to the study of sexual pheromone communication. Our understanding of the intricacies and sophistication of insect pheromone signalling has been deepened through recent work on bee sex pheromones (reviewed in Ayasse et al., 2001). Yet despite this mechanistic understanding of how

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males and females meet, there is poor knowledge of bee mating systems, namely, whether males or females are polygamous, and the extent of inbreeding, other than for a few well-characterised eusocial species (e.g. Boomsma et al., 2005; Koeniger et al., 2005).

One of the aims of this overview is to develop and make explicit a conceptual framework in which to interpret male mating behaviour of bees. Of the 20–30 000 estimated species that comprise the monophyletic taxon *the bees* (Hymenoptera: Apoidea) (Michener, 2000), only a small percentage is social. The male mating strategies of eusocial Hymenoptera have recently been reviewed (Boomsma et al., 2005). Therefore I draw examples from the more species rich solitary and primitively social bees, though noting that the framework and its inherent concepts apply equally to social as well as solitary members of this taxon. I also highlight intraspecific variability in male mating behaviour and mating systems that may confound typological thinking, and I plead for a plurality of approaches in empirical studies that will enrich our understanding of bee mating systems and their evolution.

2. CONCEPTUAL FRAMEWORK TO MALE MATING BEHAVIOUR

Male bees frequent a species-specific locality of a habitat in search of, or waiting for, mates, often at a specific time of the year and even at a specific time of the day (e.g. for *Xylocopa varipuncta*, see Alcock, 1996b; for *Apis*, see Koeniger, 1991). How can we make evolutionary sense of the interspecific diversity in rendezvous sites, and of male mate seeking behaviours employed at those sites?

Insect mating systems and male mate seeking behaviours have been the subject of a number of reviews (e.g. Thornhill and Alcock, 1983; Choe and Crespi, 1997), in some of which bees have been explicitly considered. Alcock et al. (1978), in the first major paper to place interspecific variability in male aculeate (ant, bee and wasp) mating behaviour within a Darwinian framework, highlighted two important logical premises in interpreting mating strategies; these are, that males are selected to maximise their individual reproductive success, and that receptive females are a limiting resource. Moreover, they (Alcock et al., 1978) highlighted the role of female and male dispersion in shaping male mate seeking behaviour.

More recently, and building on Emlen and Oring's (1977) seminal paper on the evolution of animal mating systems, Shuster and Wade (2003) have convincingly argued that the evolution of reproductive systems and strategies is driven by the distribution in space and time of receptive females and by female reproductive life-history, that together determine the strength of sexual selection (Shuster and Wade's (2003) *opportunity for sexual selection*). Based on these general theoretical concepts, I make explicit an evolutionary framework (Alcock et al., 1978; Ayasse et al., 2001) in which to interpret bee mating systems and male mate seeking behaviour.

2.1. Rendezvous site

For most bee species, solitary and social alike, female reproductive life-history is relatively invariant (Michener, 1974). A female emerges from its natal cell and mates soon thereafter, rapidly losing receptivity (Roubik, 1989). The rest of life is dedicated to nest construction, brood cell provisioning and egg-laying, which generally follow directly after mating. Most female halictids (Halictidae) and bumble bees (Bombini) spend a period of (winter) dormancy between mating and subsequent activities. For social species, egg-laying may be the reproductive female's (queen's) main or sole activity, at least once the first workers have emerged. For kleptoparasitic species that do not construct their own brood cells, mated females spend their post-copulatory lives in search of host brood cells to parasitise. In contrast, post-emergence males spend their entire lives in search of mates and, when necessary, in feeding so as to power mate searching activities. Male bees are generally not considered to invest in offspring, either directly by assisting in nest construction, nest defence and brood cell provisioning, or via nuptial gifts and spermatophores (cf. Cameron, 1985). To maximise their reproductive success, males will therefore be selected to maximise their access to receptive (immediate post-emergence) females.

Given the basic similarity in female reproductive life-histories across most bee species, it is the spatiotemporal distribution of receptive

Table I. Hypothesised association between the spatiotemporal distribution of receptive females (= nests) and rendezvous site.

Female (nest) density	Rendezvous site
High (aggregated)	Female emergence site (nest, nest entrance, general nesting area)
Low (dispersed)	Flowers (resource based) OR Landmark, flyway (non-resource based)

(freshly emerged) females, and hence the distribution of natal nests, that is therefore predicted to be the over-riding factor shaping bee mating system evolution and male mating behaviour. If nest density is high and female emergence more or less synchronised, males will maximise their reproductive success by searching for receptive females at nest sites where females first emerge from their natal nests (Tab. I). Where nests are dispersed and receptive (immediate post-emergence) females are therefore unpredictable in space, or for species in which female emergence is spread across time, it would not pay a male, in terms of number of matings, to await the emergence of receptive females from natal nests. Rather, rendezvous sites are expected to be at habitat locations where receptive females are more predictable, namely at flowers visited by females or at non-resource based, species-characteristic locales such as hilltops to which females are attracted for obtaining mates (Tab. I).

To what extent do the data on species' rendezvous sites fit the framework (Tab. I)? Alcock et al. (1978) suggest that the relationship between rendezvous site and nest density broadly holds across numerous aculeate species, and Table II gives examples of species mentioned in this article. At low female (nest) density, a prediction that deserves to be tested is that oligolectic bees use resource-based rendezvous sites whilst polylectic bees use non-resource based sites. This is because receptive females of oligolectic species are more predictably aggregated at their host flowers whereas females of polylectic species are likely to be more widely distributed across flowering plant species. Note, however, that two of the species with a flower-based rendezvous site in Table II are oligolectic (*Andrena agilissima* and *Macrotera* (=*Perdita*) *portalis*) whilst two are polylectic (*Anthidium manicatum* and *Osmia rufa*) (Westrich, 1989; Danforth, 1991a; Seidelmann, 1999).

The framework is not without its drawbacks. One difficulty lies in quantifying 'aggregated nesting', particularly at the scale of relevance for a bee. Another is that nest density often

Table II. Bee species mentioned in the text that can be classified according to rendezvous site and male mating behaviour. A species may occur in more than one category.

Rendezvous site	Male behaviour	
	Non-territorial	Territorial
female emergence site (nest, nest entrance, general nesting area)	*Andrena vaga* *Colletes cunicularius* *Habropoda depressa* *Lasioglossum malachurum* *Megachile rotundata* *Osmia rufa*	*Amegilla dawsoni* *Centris pallida* *Macrotera* (=*Perdita*) *portalis*
resource based (i.e. flowers)	*Andrena agilissima* *Habropoda depressa* *Osmia rufa*	*Anthidium manicatum* *Macrotera* (=*Perdita*) *portalis*
non-resource based (e.g. landmark or flyway)	*Andrena nigroaenea* *Andrena scotica* (= *jacobi*) *Apis mellifera,* other *Apis* species *Bombus hypnorum* *Bombus terrestris*	*Xylocopa varipuncta*

Table III. Predicted association between male density, male mating behaviour and other male traits related to mating.

Trait	Male density	
	High	Low
Male mating behaviour	Scramble competition	Territoriality
Large male mating advantage	Weak	Strong
Variance in male mating success	Low	High
Alternative male mating strategy	Unlikely	Likely

varies across the range of a species, confounding the characterisation of the nests of a species as 'aggregated' or 'dispersed'. Thirdly, a formal test of the framework using the comparative approach requires statistical analysis in which phylogeny is controlled (Harvey and Pagel, 1991). Yet we currently lack a rigorous phylogeny of many groups of bees (cf. Danforth, 1999; Danforth et al., 1999), particularly at deeper nodes (Michener, 2000). The Darwinian logic of the framework may nevertheless be of heuristic value in the interpretation of rendezvous sites.

2.2. Male-male competition

If the spatiotemporal distribution of receptive females is the primary factor shaping rendezvous site, then the density of males is logically of over-riding importance in dictating whether or not male territoriality in defence of a mating site is favoured by selection. Alcock et al. (1978) provide numerous arguments in support of this hypothesis. In brief, when a male can successfully defend a site at which receptive females are predictably to be found, territoriality will be favoured. If male density increases, then the costs of defending a territory against regular incursions by interloper males may, for example, engage the territorial male to such an extent that he misses the visits of receptive females to it. The number of receptive females with which he mates may be lower than those obtained by non-territorial mate searching within a rendezvous site. At high male density, scramble competition amongst males for mates will then be favoured (Tab. III).

Table II gives exemplars of species in which males practise territoriality or scramble competition, subdivided by rendezvous site.

Though male territorial species are taxonomically widely distributed (Alcock et al., 1978), non-territorial scramble competition is probably the most frequent male mate seeking behaviour amongst bee species. However, testing the framework (Tab. II) across species with respect to relative male density is fraught with the same methodological difficulties as described above for female density, namely that of quantification and that of phylogenetically controlled statistical analysis.

Despite these limitations, the framework and its inherent logic generate a number of predictions concerning male traits related to mating (Tab. III). In insects, large males are usually considered to be superior to small males in fighting for females (Thornhill and Alcock, 1983; for a refined interpretation, see Kemp and Alcock, 2003). One prediction from the framework is that there is likely to be little or no mating advantage to large male size in species that practise male scramble competition for mates. In part, this is because a male is not able to monopolise a rendezvous site (or part thereof), so there is no selection for large male size. In addition, the number of mating partners that a male acquires may be more closely related to the length of time he remains airborne and coursing a rendezvous site. Flight duration may not necessarily be related to size. For females, in contrast, fertility selection likely favours large size (Torchio and Tepedino, 1980).

Patterns of sexual dimorphism across species support the predicted relationship between male size and mate seeking behaviour. There is marked sexual dimorphism in many non-territorial species, with females larger than males (e.g. *Andrena scotica* (= *jacobi*), Paxton and Tengö, 1996), but not in territorial species, in

which males are the same size or even exceed the size of females (e.g. *A. manicatum*, Wirtz et al., 1992). Moreover, within a species there is empirical support for the notion of large male mating advantage in male-territorial species (e.g. *A. manicatum*, Severinghaus et al., 1981; Starks and Reeve, 1999), but a lack of (e.g. *Colletes cunicularius*, Larsson and Tengö, 1989; *O. rufa*, Seidelmann, 1999) large male advantage in species that practises male scramble competition.

3. MATING SYSTEM

3.1. Female monogamy

Because mating is so rarely observed in solitary bees, the assumption is that females of most species generally mate just once (Eickwort and Ginsberg, 1980). There is support from chemoecological studies of bees for this view. In the solitary bee *Andrena nigroaenea*, males are attracted by the cuticular hydrocarbon profile of virgin females, and a change in odour profile following mating is associated with a lack of attraction to mate seeking males (Schiestl and Ayasse, 2000). In the solitary bee *O. rufa*, the male himself adds odour to a female with whom he has mated that leads to her loss of receptivity and loss of attraction to other males (reviewed in Ayasse et al., 2001). Postcopulatory mate guarding by the male therefore guarantees his paternity. Though the generality of these observations and experiments has yet to be confirmed, they suggest that single mating by females may be widespread in bees.

There is, however, a lack of genetic pedigree data (genetic analysis of mother and her offspring) or behavioural observations of female mating behaviour in the field with which to support the notion of single mating by females. In the primitively eusocial sweat bee *Lasioglossum malachurum*, for example, females also lose their odour attraction to males following mating (Ayasse et al., 1999), yet genetic pedigree data indicate that females mate repeatedly (Paxton et al., 2002), which presumably they do before mating-related changes in odour bouquet. Field observations (Knerer, 1992) have also indicated polyandry in this common Eurasian bee. In contrast, the one genetic pedigree study of a solitary bee (the leafcutter bee *Megachile rotundata*) has indicated monandry (Blanchetot, 1992). If mating does lead to female odour change and loss of receptivity, their speed of onset needs to be determined.

Data on other solitary and primitively social species are clearly needed before any generalisation over female mating frequency can be made, though there are clear logistic difficulties. Firstly, many solitary species are fossorial nesters and so it is difficult to collect offspring from within a nest and assign them to a specific mother. Secondly, females of many solitary species produce few offspring, and only through genetic analysis of daughters can one determine a female's genetic effective mating frequency (Boomsma and Ratnieks, 1996). Genetic analysis of a female's spermathecal contents offers one solution to the latter problem. A full understanding of female mating strategies will require a combination of detailed behavioural observation coupled to genetic pedigree analysis.

There are better data on female mating systems for the eusocial bumble bees, honey bees (Apini) and stingless bees (Meliponini). Evidence for single mating by females of many bumble bee species is convincing (Schmid-Hempel and Schmid-Hempel, 2000), and there is good observational (Duvoisin et al., 1999) and experimental (Sauter et al., 2001) data demonstrating the role of a mating plug inserted by *Bombus terrestris* males into the reproductive tract of queens during copulation and following sperm transfer (reviewed in Ayasse et al., 2001; Colonello and Hartfelder, 2005). However, other bumble bees such as *Bombus hypnorum* (Paxton et al., 2001) are known to mate with two or more males (see also Payne et al., 2003). Honey bees (*Apis* spp.) are highly polyandrous (Koeniger et al., 2005), though stingless bees are generally monandrous (Paxton et al., 1999b; Peters et al., 1999). Arguments for and against polyandry in eusocial Hymenoptera have been discussed at length elsewhere (Palmer and Oldroyd, 2000; Crozier and Fjerdingstad, 2001; Strassmann, 2001; Brown and Schmid-Hempel, 2003).

Even if female mating frequency is currently not known for most solitary and primitively social bee species, in the vast majority of solitary, primitively social and eusocial species, females are only receptive early in adult life

(Roubik, 1989). Though it is not possible to predict how the variance in male reproductive success, and hence the opportunity for sexual selection (Shuster and Wade, 2003), varies due to polyandry *per se* in these species, the conceptual framework outlined in Table II for interpreting male mating behaviour remains valid. All categories of Table II contain both presumed monogamous and polygamous species, suggesting the lack of a relationship between female mating frequency and male mating behaviour across species. For species in which females rapidly lose receptivity post emergence, females may simply mate with sufficient males to ensure a lifetime's supply of sperm (Tarpy and Page, 2000; Kraus et al., 2004).

In a few bee species, female receptivity is thought, or known, to extend throughout adult lifespan. Well documented examples include *A. manicatum* (Wirtz et al., 1992) and *M. portalis* (Danforth, 1991a, b). Though extended female receptivity decreases the temporal clumping of receptive females and therefore would tend to place a species lower down in Table I (receptive females are less predictable in time), it is unclear how it changes the degree to which males can monopolise mates against rival males. In *M. portalis*, for example, females mate immediately prior to laying an egg in an underground brood cell, therefore the communal nest is a highly predictable location of receptive females across the entire brood provisioning season (Danforth, 1991a).

3.2. Male polygamy

Male mating frequency is poorly known, but most male bees can probably mate repeatedly. The honey bees and stingless bees are exceptions in that a male only mates once, everting his endophallus into the female genital tract during copulation, where it breaks off and remains within his partner (Starr, 1984; Roubik, 1989; Koeniger, 1991). For species with extended female receptivity (e.g. *A. manicatum* and *M. portalis*), large males are known to have high rates of copulation (Danforth, 1991a; Starks and Reeve, 1999). In ants, so-called 'ergatoid' males that mate repeatedly within the nest produce sperm into adulthood (Heinze and Hölldobler, 1993) whereas 'typical' males, that generally engage in scramble

competition for mates, only produce one complement of sperm during larval and early adulthood that is not replenished following mating, limiting the number of partners with whom they can successfully mate (reviewed in Boomsma et al., 2005). The same developmental patterns in sperm production are probably found in bees. Extended female receptivity is likely to select for life-long sperm production by males because not only will successful males mate frequently throughout life but also sperm competition (competition amongst ejaculates of different males to fertilise a female's ova) is likely to become an important determinant of a male's reproductive success (Simmons, 2001; for bumble bees, see Baer, 2003; Brown and Baer, 2005). A male that produces large numbers of sperm is likely to be favoured in sperm competition.

4. INTRASPECIFIC VARIABILITY

To what extent do all males of a species follow the same male mating behaviour? To what extent are the mating systems of males and females invariant within a species?

The answer to the former question is that intraspecific diversity in male mating behaviour has frequently been documented (e.g. Alcock et al., 1978; Stone et al., 1995; Willmer and Stone, 2005). Table II contains some species in two categories. Following the logic of Shuster and Wade (2003), male territoriality and large male mating advantage are likely to increase the variance in male mating success (compared to species practising scramble competition), greater opportunity for sexual selection and for the evolution of alternative male mating strategies (Tab. III). In support of these ideas, two well studied male-territorial species also exhibit alternative male mating strategies (Tab. II); in the solitary *A. manicatum* (Villalobos and Shelly, 1991; Starks and Reeve, 1999) and the communal *M. portalis* (Danforth, 1991a), large males monopolise matings at flowers or within the communal nest, respectively, a single male maintaining a territory for days on end. Small males follow an alternative strategy of patrolling vegetation or flowers, respectively, in search of receptive females. Intraspecific male dimorphism (and presumably alternative mating strategies) is

also associated with male territoriality across a group of Australian colletid bees (Alcock and Houston, 1996).

However, alternative male mating strategies linked to male size are also known in other bee species that do not exhibit marked male territoriality. In *Amegilla dawsoni* (Alcock, 1997) and *Centris pallida* (reviewed in Thornhill and Alcock, 1983), for example, large males search for receptive females at natal nests, where they course over a nesting aggregation yet fight to gain access to a freshly emerging female. Smaller males patrol surrounding vegetation in search of mates. Hence even in cases of what superficially appears to represent male scramble competition, males may fight for mates and establish a temporary territory around an emerging female. Studies on additional species are needed to determine the generality of the scheme outlined in Table III. Specifically, is it only in male territorial bee species that high variance in male mating success leads to the evolution of alternative mating strategies?

Greater appreciation of intraspecific diversity in male mating behaviour may well lead to its discovery in many more species, particularly those known to practise male-territoriality. This would open up study of the evolutionary origins of intraspecific diversity in male mating behaviour or morphology (Danforth and Desjardins, 1999). An important and still open question is the extent to which interindividual variation in male behaviour is genetically determined or is conditional upon environment (e.g. larval diet or size).

Some examples from my colleagues' and my personal researches highlight intraspecific variability in the mating system. *Andrena agilissima* males practise scramble competition for females at flowers, where mating is observed (Westrich, 1989). Yet we have also demonstrated that most (97%) females of this communal nesting bee first emerge from their underground natal nests in spring with a full spermatheca (Paxton et al., 1999a). Clearly, males (and females) of this communal species utilise at least two mating sites, within the nest and at flowers. A similar phenomenon occurs in *A. scotica*, a species in which males course hedges in search of females (Tengö, 1979). Over 70% of *A. scotica* females have been recorded to mate intranidally (Paxton and Tengö, 1996). The classification of a species as fitting into one of the categories of Table II may be too simplistic; use of two or more rendezvous sites may be widespread among bees (e.g. *O. rufa*, Seidelmann, 1999).

For both *A. agilissima* and *A. scotica*, there are no known size differences among males in their morphology that would suggest specialisation on mate searching at one or other mating site, whereas there are for *A. dawsoni*, *A. manicatum*, *C. pallida*, and *M. portalis*. In *A. agilissima* and *A. scotica*, a male may opportunistically mate intranidally during emergence from its natal cell and nest, or it may use the presence of post-emergence females as a cue to concentrate its mate searching at a specific rendezvous site. Behavioural observations of the solitary bee *Habropoda depressa* indicate that even a single male may use multiple rendezvous sites in search of mates (Barthell and Daly, 1995). Again, rejection of typological thinking may lead to a greater realisation of the range of behaviours exhibited by males (and females) in securing a mate.

4.1. Inbreeding

Mating in the honey bee *A. mellifera* never occurs within the colony but at flyways or 'drone congregation areas' (Koeniger, 1991; Koeniger et al., 2005), a pattern of mating that has probably evolved as a means to reduce inbreeding (Page, 1980). The deleterious effects of consanguineous mating are profound for haplodiploid species like *A. mellifera* with complementary sex determination (CSD, Beye et al., 2003) because inbreeding leads to the production of diploid males that are usually considered sterile. All bee species are thought to possess CSD (Cook and Crozier, 1995), though conclusive evidence for it comes from just a few (*A. mellifera*, see Beye et al., 2003; and *Bombus terrestris*, see Duchateau et al., 1994). By inference, all bee species are therefore likely to have evolved mating systems and behaviours that reduce inbreeding.

There is some support for this view. Males of several *Bombus* species collect at nest entrances to enter and mate with newly emerged gynes whilst the colony's own males are evicted soon after eclosion from the nest by the workers (Plowright and Pallett, 1979; Foster, 1992). This pattern of male eviction has probably evolved to reduce inbreeding

because, in other *Bombus* species that mate outside the nest, workers do not evict nestmate males. High diploid male production (and the concomitant loss of daughters) has even been advanced as a factor limiting the evolution of sociality in the Neotropical orchid bees (Roubik et al., 1996; Zayed et al., 2004; but see Takahashi et al., 2001). Yet *Euodynerus foraminatus*, an aculeate wasp that regularly practises inbreeding coupled to CSD, appears to suffer little cost of inbreeding because diploid males are fertile and produce 'normal' haploid sperm (Cowan and Stahlhut, 2004).

The two fossorial and communal *Andrena* species listed in Table II, *A. agilissima* and *A. scotica*, frequently mate intranidally as well as at extranidal rendezvous sites. For the latter species, there is good genetic support for inbreeding linked to intranidal mating (Paxton et al., 1996), probably a consequence of consanguineous mating within the natal nest before first emergence in spring. We lack genetic data on *A. agilissima* to know if inbreeding is a significant component of its mating system. However, in the fossorial and solitary *Andrena vaga*, genetic data have also demonstrated a high level of inbreeding (Mohra et al., 2001). Though the choice of species in these *Andrena* studies was not random, they were selected independently of their mating system. I therefore suggest that inbreeding, because it occurs within the natal nest and out of sight, may be considerably under-recorded among bees. Furthermore, combining behavioural observations with genetic analyses clearly provides a more profound understanding of the mating system(s) of a species.

If inbreeding was more widespread in bees than currently acknowledged, mechanisms of sex determination at the genic level may be different to single locus CSD, or diploid males may not be sterile or represent a genetic load to the population. There may be a need to treat with caution diploid male production as a general measure of inbreeding and population size in bees (Packer and Owen, 2001; Zayed et al., 2004).

5. CONCLUSIONS

Despite their diverse rendezvous sites and mating strategies, male bees exhibit mate seeking behaviour that can be broadly placed within the conceptual framework proposed in Table II, facilitating its evolutionary interpretation. However, the utility of bees as models in the inductive approach of generating general theories of mating systems and strategies will be limited by the difficulties in rearing them and experimentally investigating their mating behaviour in the laboratory. This is because most bee species are univoltine or are active during only a brief, species-specific period of the year. Also, mating may occur in an environmental setting that is difficult to replicate in the laboratory. Their diversity and suitable size for individual observation nevertheless make them useful models in the deductive approach of testing general theories concerning male mate seeking behaviour and mating systems.

Where is there most need for additional data? In many instances, the presence of large numbers of males in search of females at a specific locale has been taken as evidence for mating at that site, even though females may have been rarely observed and mating may never have been recorded there (Tengö, 1979). For many bee species, there is clearly a need to confirm where, when and how often females mate. The same is true for males (Boomsma et al., 2005). One relationship that deserves closer inspection is the impact of sociality on mating behaviour and mating systems, for which bees, given their diversity in social organisation (Michener, 1974), are ideally suited. Interspecific comparison of male bee mating behaviour is hampered by the lack of a robust phylogeny for many taxa. Rather, we can expect further advance in our understanding of those factors shaping male bee mating behaviour and mating systems to come from intraspecific studies of species in which considerable diversity within and between individuals has been documented, an approach that has been championed by Alcock (e.g. 1996a).

Résumé – **Comportement d'accouplement des mâles et systèmes d'accouplement chez les abeilles : vue d'ensemble.** Les Apoïdes se caractérisent par une diversité interspécifique énorme concernant aussi bien les lieux d'accouplement, où les mâles recherchent les femelles, que les stratégies utilisées par les mâles pour s'assurer des accouplements efficaces. Je décris ici un cadre conceptuel qui pourrait être à la base de l'évolution de ce comportement. Il repose sur la logique de Darwin et les propositions de von Alcock et al. (1978) et de Shuster et Wade (2003) et permet d'interpréter les différences interspécifiques du comportement d'accouplement des mâles. La répartition des femelles, prêtes à s'accoupler dès leur émergence, est d'une importance décisive pour la mise en place des lieux d'accouplement. C'est pourquoi la répartition des femelles équivaut le plus souvent à la répartition des nids (Tab. I). Lorsque la densité des nids est élevée, on peut s'attendre à ce qu'il existe une pression de sélection pour les accouplements à proximité des nids. Si par contre les nids sont dispersés, il est probable que les lieux d'accouplement se mettront en place de préférence près des sources de nourriture (fleurs) ou près d'endroits indépendants de la nourriture (lignes de vol ou lieux de rassemblement). On donne des exemples pour ces deux cas (Tab. II).

C'est la densité des mâles en compétition qui vraisemblablement favorisera le plus l'un des deux facteurs : la territorialité des mâles ou la compétition par la ruée (Tab. III). Les observations coïncident en grande partie avec le cadre proposé. Néanmoins ses limitations sont soulignées et de futurs axes de recherche proposés.

Mis à part les abeilles mellifères du genre *Apis*, dont les femelles s'accouplent avec de nombreux mâles (polyandrie), on considère que les femelles de la plupart des espèces d'Apoïdes ne s'accouplent qu'une seule fois (monoandrie), bien que les données génétiques pour soutenir cette assertion soient généralement manquantes.

J'attache une valeur particulière à la description de la diversité intraspécifique des lieux d'accouplement, du comportement des mâles et du système d'accouplement qui est en partie prédite par le cadre conceptuel. En me basant sur les données empiriques de trois espèces d'*Andrena*, je suggère que la consanguinité peut être beaucoup plus répandue chez les Apoïdes, en particulier chez les abeilles nidifiant dans le sol, qu'on ne l'a admis jusqu'à présent. Le cadre conceptuel peut aider à interpréter le comportement d'accouplement des mâles et les systèmes d'accouplement chez les abeilles, mais aussi à produire des prédictions, qui devront être testées dans les recherches à venir. Il est nécessaire de disposer d'une combinaison de données comportementales et de données génétiques pour avoir une vue plus complète des systèmes et des stratégies d'accouplement chez les abeilles.

Apoidea / lieux d'accouplement / compétition par la ruée / territorialité / consanguinité

Zusammenfassung – **Paarungsverhalten von Männchen und Paarungssysteme der Bienen – eine Übersicht.** Die Apoidea zeichnen sich durch eine erhebliche zwischenartliche Vielfalt aus. Sowohl bei den Paarungsplätzen, wo Männchen nach Weibchen suchen, als auch beim Verhalten der Männchen und ihren Strategien zur Erreichung von erfolgreichen Paarung gibt es eine hohe Diversität. Ich beschreibe hier ein System, das der Evolution dieses Verhaltens zugrunde liegen könnte. Dieses Systems beruht auf Darwin's Logik und Vorschlägen von Alcock et al. (1978) und Shuster and Wade (2003) und erlaubt die Interpretation von interspezifischen Variationen im Paarungsverhalten der Männchen. Eine entscheidende Bedeutung für die Entwicklung von Paarungsplätzen ist die Verteilung von Weibchen, die typischerweise direkt nach dem Schlupf paarungsbereit sind. Deshalb ist die Verteilung der Weibchen meist gleichbedeutend mit der Verteilung der Nester (Tab. I). Bei dicht beieinander liegenden Nestern ist zu erwarten, dass ein Selektionsdruck für Paarungen in der Nähe der Nester besteht. Sind die Nester jedoch verstreut, ist es wahrscheinlich, dass sich bevorzugt Paarungsorte an Futterstellen (Blumen) oder an von Futter unabhängigen Orten (Flugbahnen oder Sammelplätze) entwickeln; Beispiele für beide Typen werden angeführt (Tab. II).

Die Dichte der konkurrierenden Männchen hat wahrscheinlich den größten Einfluss darauf, ob Männchen Territorien verteidigen oder ob „scramble competition" bevorzugt auftritt (Tab. III). Die Beobachtungen stimmen in hohem Maß mit dem vorgestellten System überrein, dennoch werden deren Grenzen deutlich aufgezeigt, und Anleitung für zukünftige Forschungen gegeben.

Anders als Honigbienen, deren Königinnen mit sehr vielen Drohnen kopulieren, paaren sich die Weibchen der meisten Bienen vermutlich nur einmal. Allerdings fehlen hierzu bei vielen Arten noch genetische Daten. Die Männchen dagegen können im allgemeinen mehrere Weibchen begatten, wenn sie die Gelegenheit dazu finden. Ich lege besonderen Wert auf die Beschreibung der innerartliche Diversität der Paarungsplätze, des Verhaltens der Männchen und des Paarungssystems, das zum Teil auf Grund des Konzepts vorausgesagt wurde. Empirische Untersuchungen von 3 *Andrena* Arten lassen mich vermuten, dass Inzucht wahrscheinlich viel häufiger vorkommt als bisher angenommen, besonders bei bodennistenden Bienen . Das hier vorgestellte Konzept könnte bei der Interpretation des Paarungsverhaltens der Männchen und des Paarungssystems von Bienen helfen, ist aber auch zur Entwicklung von Vorhersagen geeignet, die in zukünftiger Forschung getestet werden sollten. Eine Kombination von Daten über Verhalten und Genetik ist notwendig, um ein zuverlässiges Gesamtbild über Paarungssystem und -strategien bei Bienen zu erhalten.

Apoidea / Paarungsplätze / scramble competition / Territorialverhalten / Inzucht

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