Advanced article

Ecology and Social Organisation of Bees

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Social behaviour of multiple females sharing a nest has been documented for two bee families, seven tribes and genera including over 2000 species – 8% of all non-parasitic bees. Early in social bee evolution, a single female produced a female that became her nest helper. Brood protection, larger reproductive output, or female longevity benefited the coexisting females. Many social bees live in tiny colonies and demonstrate elasticity in behaviour and reproductive options. Larger colonies ultimately evolved permanent castes – females unable to forage, build or defend a nest – and sterile helpers, and also evolved foraging coordination and honey storage. The colonies have stringent nesting requirements and advanced defensive behaviour, including stinging, biting and chemical defense, but also protected nest sites, timidity and crypsis. Advanced sociality was reached by Meliponini in Cretaceous times, and Eocene by Bombini and Apini. Other Apidae had some social behaviour since mid Cretaceous, as did Halictidae since Miocene, and both repeatedly lost it. Scarce resources and short flowering seasons force many kinds of social bees to enter diapause or disperse. In tropical forests, where highly social bees predominate, colonies of *Apis* are migratory and meliponines display aggressive foraging, regulated nesting or infrequent reproduction.

The Birth of Bee Societies

Bees evolved not to be social but to be efficient, a trait embedded in their ecology. An overwhelmingly solitary group, bees are haplodiploid, with males arising from unfertilised eggs and therefore having only one set of chromosomes, from the mother, rather than one from each parent (Crozier and Pamilo, 1996; Michener, 2007). Most bee species live in temperate climates, whereas most social bee colonies exist in the tropics. Almost all temperate-zone bees have a single annual generation during the flowering season. However, some in the temperate zone, and many in the tropics, have multiple annual generations, and relatively long-lived females. That evolutionary grounding permitted the advance and retreat, and eventual culmination with extreme specialisation, of bee sociality. Presumably, if colonies are too costly to maintain or the females and males comprising them do not act in a productive and coordinated manner, then natural selection maintains the original 'plan' for a bee. A female makes a nest, provisions individual brood cells with pollen and nectar, lays her eggs there and dies. Males do not serve to maintain the nest but forage and exist primarily as reproductive entities.

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Social interactions – 'sociality' – is obligatory for most social bee species, but their diversity in terms of behaviour, ecology and physiology is extensive. Such diversity in biological groups often arises as a result of antiquity and persistence through changes undergone by the earth as a whole. The bees that evolved large colonies and uniform sociality are exclusively tropical, and most social bees within temperate climates have a colony, initiated by a single female or small group, which lasts for a relatively short time and then disbands. A large colony of the Western hive bee *Apis mellifera* (not exclusively tropical but with an origin in tropical Africa and its core population there) may endure for decades in a secure nesting cavity (Seeley, 1995), whereas little nests of *Euglossa*, a tropical 'orchid bee' and some allodapine carpenter bees, last a few months and include only two interacting females. A significant behaviour among the most advanced social bees, the meliponines and apines, is the ability of colonies to find and exploit floral food by recruiting nestmates (**Figure 1**, **Figure 2**, **Figure 3** and **Figure 4**), linked to the ability of producing and storing honey (see below). **See also**: Terrestrial Ecosystems in the Past 100 Million Years

There have been multiple routes to sociality and adaptive social paradigms that may stand or fall with the environment in which bees live (see Wcislo and Tierney, 2009; Cardinal and Danforth, 2011). The world climate cooling during the Eocene (*ca.* 35 million years ago, Mya), for example, permitted the evolution and dispersal of cold-adapted bumble bees (Hines, 2008). The fracturing of Gondwanaland into African and South American continents permitted global dispersal of meliponines – the largest

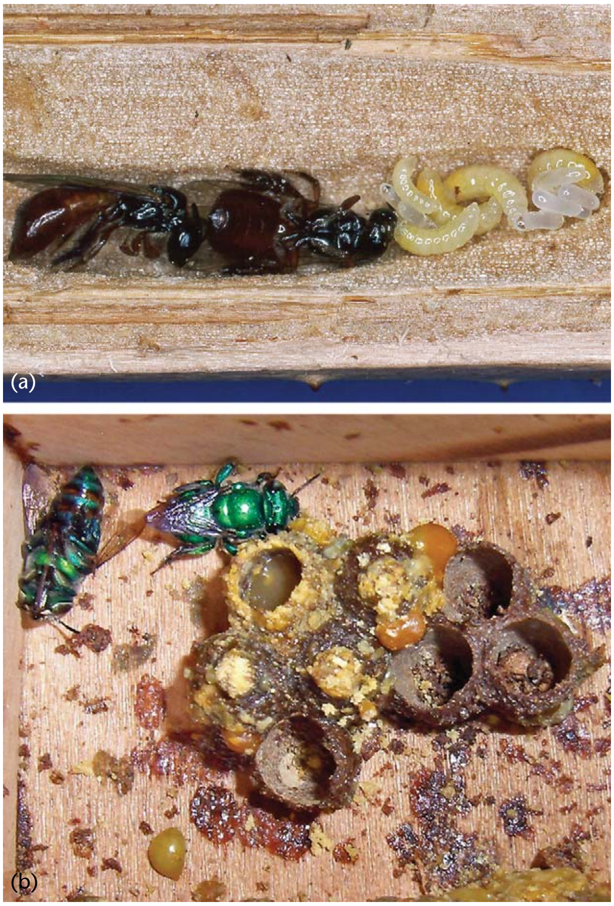

Figure 1 (a) Colony of *Exoneura* (Allodapini), in Borneo (courtesy of M.P. Schwarz). (b) Colony, one live and one dead female, brood cells, of *Euglossa hemichlora* (Euglossini), in Panama.

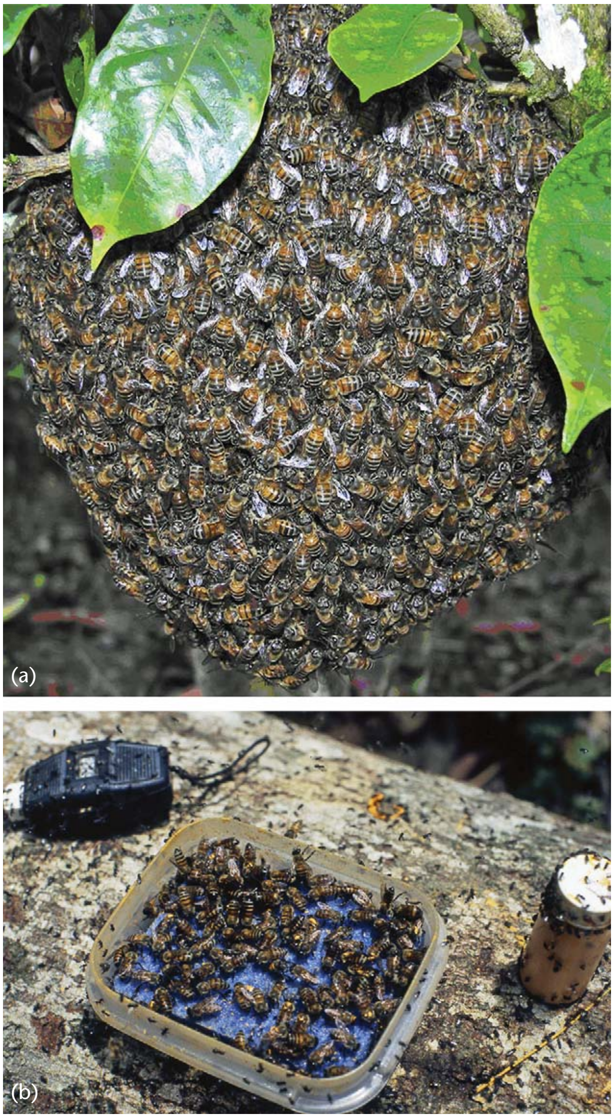

Figure 2 (a) Dispersing colony (absconding swarm) of Africanised *Apis mellifera*, in Panama. (b) *A. mellifera* and *Hypotrigona* (Meliponini) recruiting colonies to sugar water bait, in Gabon.

group of advanced social bees – 100 Mya (Rasmussen and Cameron, 2010). Finally, the 'hive bees', familiar to all and the most studied and economically useful single insect on the planet, were the result of changing climates that allowed a tropical honey bee to evolve adaptations to cool climates in Europe and elsewhere, during glaciations in the not too distant past (Ruttner, 1988; Oldroyd and Wongsiri, 2006).

How is Bee Sociality Recognised?

Social bees are not underrepresented among bees in general, and they range across major bee groups. The social behaviour of multiple females sharing a nest has been documented for two bee families (Halictidae and Apidae), seven tribes and genera composed of well over 2000 species – approximately 8% of all nonparasitic bees. The bee families Colletidae, Megachilidae, Stenotritidae, Andrenidae and Melittidae lack social species.

Social bees must nest together. That is, females must live much of their adult lives within the confines of a structure that they have selected, and usually significantly modified or built, for producing brood. The nesting female cohabitants are in close physical contact and must act, as adults, in ways that the totipotency of one individual is, at least temporarily, compromised. Nonetheless, it is not necessarily an absolute sacrifice or altruistic act that defines sociality. It may be that no other behaviour would fit the setting, that is, the bees are doing more than merely getting by – they are 'making the best of a bad situation' or, literally 'waiting until things improve'. Such instances arise when, for example, one female has not been able to mate, whereas her nestmate has, or one female has not been able to establish a nest, but is 'tolerated' by another female with a nest (see Batra, 1966).

Why one bee should tolerate another in its nest is a subject worthy of extended consideration (Michener, 2007;

Figure 3 (a) The nest entrance of *Paratrigona ornaticeps* (Meliponini), in Panama. (b) The nest entrance of *Homotrigona fimbriata* (Meliponini) fallen from a forest tree trunk, in Brunei.

Breed and Buchwald, 2009; Wcislo and Tierney, 2009; Tierney *et al*., 2008) for such associations can lead to parasitism. Among the bees, one female may use the provisions of another female to rear her own brood, or consume the egg a female has placed on pollen for her own young, and replace it with an egg of her own (Michener, 1974; Roubik, 1989). This behaviour exists in roughly 15% of all bee species, the great majority of which are solitary. In both solitary and social bees, it is a terminal evolutionary stage, with no possibility of regression to a 'free-living' lifestyle. However, among the social parasites, there are facultative species and individuals among allodapine bees, which are also capable of independent nesting and reproduction (Tierney *et al*., 2008) and something akin to this exists also in orchid bees (Roubik and Hanson, 2004).

Parasitism is not uncommon among social bee groups. The allodapines, a tribe not as large as the halictines (see below) but considerably older, evolved social parasites 11 times (Tierney *et al*., 2008). Euglossines evolved parasites at least twice (two of the five genera, Ramírez *et al*., 2010a, b; Cardinal *et al*., 2010), *Bombus* once (Williams *et al*., 2008), halictines nine times (summary in Cardinal *et al*., 2010) and *Apis* not at all – although they do steal food from each others' nests (Ruttner, 1988; Roubik, 1989). That phenomenon also exists in the meliponines, in which there are roughly 23 parasitic species (*Lestrimelitta, Cleptotrigona, Trichotrigona*) that use brood provisions or building materials of multiple host species (Roubik, 1989, 2006; Camargo, in Vit *et al*., in press; Camargo and Pedro, 2007). The Apidae (one of the seven families of bees now living) is, alternatively, believed to have evolved parasitic lineages only four times (Cardinal *et al*., 2010), but this interpretation, along with that given for the parasitic orchid bees, which are basal in euglossines (Ramírez *et al*., 2010b) need further study – it is extremely difficult to piece together evolutionary histories of groups in which entire tribes have gone extinct, along with many genera and evolutionary alternatives to what we now encounter. The foregoing studies and conclusions were in large part discoveries based upon molecular phylogenetics, which makes use of different genes and different patterns of change and evolution that each reveals. A 'molecular clock' approach has been applied in this work, which is used to trace a rate of divergence between bees within the 'tree of life'. The degree of difference in gene components (base pairs) is judged from neutral mutations which arise at a standard rate, calibrated by a firm date given from fossil or biogeographic data. However these insights are interpreted, they are extraordinary. For example, cleptoparasitism is an ancient behaviour in apid bees that first evolved 95 Mya, 60 million years (My) earlier than evidence from fossils would indicate, like simple social behavior (Rehan, *et al*., 2012). **See also**: Diversity of Life through Time; Molecular Clocks; Molecular Clock: Testing

The terminal stage of sociality in bees is also an absolute with no possibility of regression, although advances in study and interpretation of social behaviour provide credible reasons that bees need not be driven to that stage. The females are 'castes', either able to produce only male eggs (if any eggs are laid at all) or lay both male (haploid) eggs or fertilised, female (diploid) eggs. The former are sterile 'workers' and the latter are termed 'queens'. I doubt

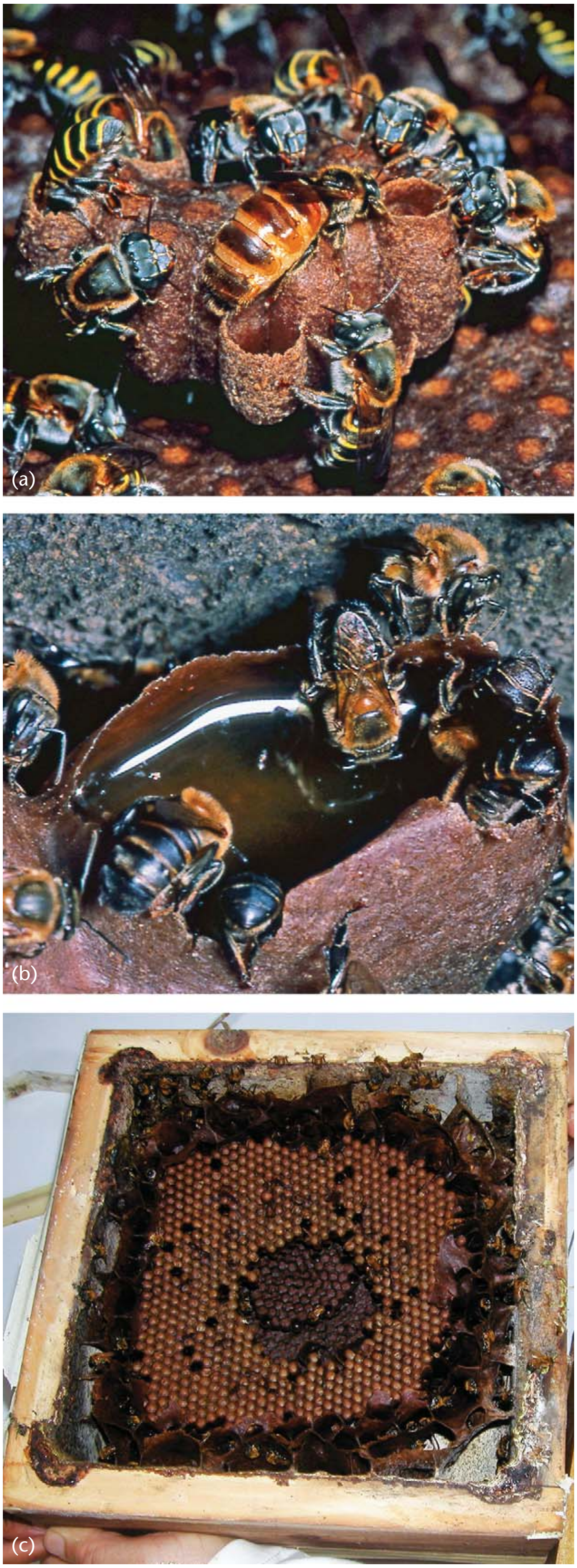

Figure 4 (a) Queen and workers of *Melipona triplaridis* (Meliponini) on brood comb, in Panama. (b) Workers of *Melipona panamica* (Meliponini) ripening nectar in nest, honey storage pots, in Panama. (c) Hive of *Melipona*, in Colombia.

there is a biological difference in the amount of labour or effort either group realises during its life, but these terms are traditional.

The estimated 500 stingless bee and 12 honey bee species share those rarest of bee social adaptations – polymorphic females – and have no solitary phase (**Table 1**). In contrast to the bumble bees – a highly female-polymorphic lineage characterised by lone queens that nest and provision brood cells – a meliponine or apine queen must use a nest built by a group of workers, and she cannot feed herself. The gravid queen of a meliponine cannot even fly. Yet these species are dominant among bees in the richest terrestrial ecosystems (Roubik, 1989; Roubik *et al.*, 2005).

As exemplified by any remarkably complex and complete evolutionary innovation – and advanced social behaviour by a small insect is certainly one such feat – the steps taken to arrive at that status have been obliterated by the extremity of biological divergence over time. To help retrace the processes of social evolution in bees, living examples recognised as intermediate in their sociality are highly valuable (Schwarz *et al.*, 2007; Wcislo and Tierney, 2009; Rehan *et al.*, 2012; Cardinal and Danforth, 2011; Michener, 1974). Bees with options or 'elasticity' to move back and forth, between different possible expressions of sociality due to their genes and environment, are most noteworthy in Halictini or 'sweat bees'. These are per force the largest group of social bees, having over 800 species. They evolved social genera or lineages three times. They 'downgraded' sociality 12 times, as Xylocopini and Euglossini have also lost simple social behavior (Rehan *et al.*, 2012).

Halictines occasionally display different degrees of sociality during ontogeny, as they progress from females of the same generation (semisocial colonies) to those of overlapping (mother and daughter) generations; the latter is termed eusocial organisation. Some halictine females mate and then enter dormancy at the end of the temperate zone summer, to emerge the next spring and form nesting groups with females of the same generation, among which one usually becomes established as the dominant, egg-laying, female. One species, *Halictus sexcinctus*, is even eusocial, solitary and communal. It is important to clarify the last term – it implies a total lack of cooperation between females nesting close together. Close study and inspection of females sharing a nest aggregation is needed to produce convincing evidence that no cooperation occurs between them, for otherwise independent females share building material and there are occasional instances of two or more females contributing to the food and material of a single brood cell (see below). But that observation means little because, although females are cooperating for a period of time, one female may replace a competitor's egg with her

Table 1 Social bees, their estimated number of species, and taxonomy

Name	Common name	No. of social species[a]	Genera[b]
Halictini (Halictidae)	Sweat bees	830	*Halictus, Lasioglossum, Augochlora, Augochlorella, Augochloropsis, Megalopta*
Bombini (Apidae)	Bumble bees	250	*Bombus, Bombus (Psythirus)*
Euglossini (Apidae)	Orchid bees	140	*Euglossa, Eulaema*
Xylocopini (Apidae)	Carpenter bees	10	*Ceratina, Xylocopa*
Allodapini (Apidae)	allodapines	250	*Exoneura, Hasinamelissa, Braunsapis, Halterapis, Exoneurella, Macrogalea*
Apini (Apidae)	Honey bees	12	*Apis*
Meliponini (Apidae)	Meliponines or Stingless bees	500	*Trigona, Melipona, Scaptotrigona, Oxytrigona, Plebeia, Trigonisca, Cephalotrigona, Lestrimelitta, Scaura, Paratrigona, Tetragona, Meliponula, Cleptotrigona, Dactylurina, Liotrigona, Hypotrigona, Lepidotrigona, Tetragonula, Heterotrigona, Lisotrigona, Pariotrigona, Austroplebeia*

[a] Estimates from cited literature.
[b] Selected genera for allodapines and meliponines.

own. Moreover, one female may take over the nest when the dominant female or mother dies. Another term that has useful application is quasisocial, which applies to a colony in which all females have mated and are fecund. That is a basic association from which facultative social parasites may arise.

Environmental triggers regulating change in a bee's social status or a colony's social organisation certainly exist. Not surprisingly, different social organisations within a single species occur in the temperate zone, where seasons change and ecological transitions occur more frequently than in the tropics. Halictine bees of high elevation in temperate North America are less social than the same species in lower elevations (Yanega, 1988). Allodapine bees, with over 250 species, all are tropical. *Xylocopa* often have multiple annual generations and nest in colonies in the tropics, but display neither in the temperate zone (Rehan *et al.*, 2012). Although they resemble halictines in many ways, they generally are social throughout their lives (Schwarz *et al.*, 2007). One may postulate that permanence of sociality results from relative absence of severe annual climate fluctuation. The sustenance of a colony, always including honey in the stingless bees (Meliponini) and honey bees, necessarily includes flowering that is sustained or intensive during much of the year. Such community-level flowering 'phenology' also is driven by climatic conditions. Flowering is often most intense during the dry season (in areas with relatively high annual rainfall), or following a brief rainy period, in dry or desert-like areas.

There were social bees among the common ancestors of the bumble bees (Bombini) and stingless bees (Meliponini) in the Cretaceous, 100 Mya (Kawakita *et al.*, 2008; Hines, 2008; Rasmussen and Cameron, 2010, but see Cardinal and Danforth, 2011) and there were entire tribes, among their descendants, that went extinct, but which left a fossil record from the Palaeocene, in Baltic amber fossils 44 Mya (Engel, 2001; Cardinal *et al.*, 2010). Among allodapines, although none is advanced and eusocial, sociality is ancestral and dates from a time between 50 and 80 Mya (Tierney *et al.*, 2008); genera with distinct castes exist, and full sociality (for this group) evolved 50 Mya (Dew *et al.*, 2011). The bombines evidently consolidated as a social group 34 Mya (Hines, 2008). All social Apidae, including the carpenter bees, both large and small (the allodapines are sometimes called little carpenter bees, with Ceratinini, whereas *Xylocopa* are the large carpenter bees), the meliponines, apines and bombines may have a common social ancestor, rooted in the mid Cretaceous (Cardinal and Danforth, 2011). To clarify that all social bees are not a single lineage, halictines provide the key data as the newest group, including those with queen-like and worker-like individuals, as well as species that are facultatively social

(Michener, 2007). A Miocene fossil honey bee, presumably highly social since its morphology coincides with that of the living species, is an older lineage. It was recently discovered as a fossil in North America, but had a geographic origin in the Old World tropics in early Eocene times (see Lo *et al.*, 2010).

Although there is little doubt that all social bees did not descend from a single social ancestor, it seems likely that we do not have all the pieces of the 'puzzle' (see Darwin, 1859) of bee sociality. Why are there altruistic females, who do not strive to have personal offspring? Inclusive fitness (which involves not only personal reproductive fitness but also helping a relative, who shares familial genes, to reproduce) and kin selection (measured by an individual's total contribution to the gene pool, brought about in part by its social interactions) are thought sufficient. Many authors have dissected and described, often with mathematical formulae, the potential natural selection advantages to individuals within groups, to describe what we observe in social bees or other social animals. The kin selection models are based on what degree of relatedness (genes in common) exist between individuals, how much help is given between them, how much personal versus shared reproductive success is realised, and how many male or female individuals (haploid and diploid) are produced. Males usually mate only once, and pass on their genes through a single female. If a male mated with a queen, then she will sire many offspring, but if she is a solitary female, her eggs are fewer, whether her female progeny are sired by multiple males or not. With the exception of *Apis* (in which queens mate with 10–30 males) a single mating by a female is, by far, the rule among the social bees (Peters *et al.*, 1999; Zimmermann *et al.*, 2009). Any attempt to model the genetic intricacies of a genealogy from descendants of a single mother, singly or multiply mated, is problematic. The honey bees can have multiple males sire the workers of a single colony because there are potent chemical mechanisms for social cohesion to prevail (Seeley, 1995). It seems doubtful that other social bees, including the meliponines, could evolve a comparable biology.

There may have been other social bee tribes or groups that wavered on the brink of extinction and then finally were no more. This conjecture need not impair our efforts to reconstruct the probable evolution of bee sociality by inspecting the cluster of traits that surround the social species, but appear seldom or never among other bees in the

Table 2 Correlates and putative causal agents of bee sociality

	Value or correlate	Present bee group	Special adaptation
Haplo-diploidy	High female relatedness	All	
Female-biased sex ratio	Worker control	B, E, H	
High predation/parasite pressure	Guarding behaviour by queen or helper	AL, H, M, A, E, C	
Wax production	Nectar, pollen hoarding and honey production	M, A, ∼B	
Abundant nesting material (resin)	Material for defense and food storage	M, E, A	
Mating limitation	Default helpers	AL, H, E	
Worker 'policing'	Inclusive fitness favors queen control	B, A	
Single mating	Kin selection favors queen control	M, B, AL, H, C	
Multiple mating	Adaptability and social conflict	A	All *Apis*, rare in *Bombus*, halictines, meliponines
Food scarcity	Short-term colony	B, H, E	
Female longevity	Generation overlap	A, H, M, A	
Nest re-use	Generation overlap	C, AL, ∼B, E, M, A	
Brood care and feeding	Cooperation and mutualism, or policing	AL, C, E	
Mutual female tolerance	Incipient colonies	H, A, ∼M, ∼E	
High relatedness or population viscosity and limited dispersal	Kin selection	AL, H, M, A	
Long flowering season	Multivoltinism and generation overlap	M, A, E, AL	
High resource abundance	Competition and hoarding ability	B, A, M	*Bombus*, high latitude summer effect
Loss of sting	Multiple queens	M	meliponines
Female polymorphism	Dominance hierarchy	H, B, M, A	halictines, allodapines

estimated 30 000 species (Michener, 2007). In **Table 2**, I have given some characteristics that several authors suggest are key factors in bee social evolution. With some imagination they could also be ascribed to extinct social groups, known from the quite limited but fascinating bee fossil record. Although we plainly can never grasp the total breadth of social bee evolution, the intrinsic behaviour and environmental features that have clear correlates (not implying necessary causation) with the degree of bee sociality can be listed and addressed.

How is Bee Social Behaviour Organised?

A few of the important principles in bee societies of any size or duration are kin recognition, division of labour, task allocation and colony feedback. A guard bee is imprinted with the odour of itself and nestmates (Breed and Buchwald, 2009) so that it may recognise and repel intruders. These may even include other bees of the same species. In fact, all social bees must interact with parasitic bees, either other genera, closely related species, or conspecifics that specialise in stealing or usurping food or material, and even those that usurp the nest and kill the host colony (Roubik, 1989). A lack of close relatedness and frequent aggressive or parasitic conflict between females in euglossine societies may be one of the primary factors leading to failure of advanced sociality in this group (Roubik *et al.*, 1996; Cardinal and Danforth, 2011).

Division of labour in bee colonies occurs among the primary reproductive and her helpers. Each has certain tasks to perform, in order that the colony survive and reproduce. If one wonders why colonies are more adaptive and advantageous among bees that may be either social or solitary, certain lines of inquiry lead to a convincing answer that colonies are, 'better'. In the allodapines, euglossines and halictines, almost none of which possess advanced social organisation including castes, a larger number of cooperating females produces larger output of males and reproductive females, but not a larger *per capita* production. The conclusion I see from this result is that the colony is the unit of selection, not the efficiency of an individual within it. Thus, seemingly contradictory to the initial statement of this essay, efficiency is defined in terms of individuals among solitary bees and colonies for social species. The repeated success of colonies in leaving descendants, and repeated failure of individuals, however efficient, must have given rise to increasing sociality in bees.

Female polymorphisms are extreme in some social species, apart from the large size of a queen compared to workers. A large female may be an excellent nest defender by blocking the nest entrance hole with her head, or pointing her sting in the direction of a nest intruder (Batra, 1966). A forager can bring food and also guard the nest, when she is a primary reproductive, or while the primary reproductive guards the nest. Such guarding may be doubly adaptive because the primary reproductive can insure no other mated females, or none that are not her own offspring, enter the nest (Schwarz *et al.*, 2007). In the advanced bee societies, the workers of *Bombus* are unique for ranging in size from small to queen-like individuals, although usually none is quite as large as the queen. Interestingly, the successive individual females reared by the queen *Bombus* become larger as the season progresses, and culminate with the production of future, totipotent, queens (Benton, 2006; Goulson, 2010). By their differences in morphology and primarily the feeding apparatus for extracting nectar – their tongue, or proboscis – they comprise a unit of diversity in pollinating and foraging unrivalled by any other kind of bee colony.

The honey bees and meliponines constitute an impressive example of behaviour programmed by age. Although worker bees are totipotent in the tasks that they are able to perform, some spend most of their lives doing one thing. On the average, however, younger bees clean the nest, feed the queen, prepare and provision the brood cells, and maintain the exterior and interior portions of the nest. Older workers orchestrate foraging activities by receiving food from incoming bees and increasing or stifling the demand for foragers to seek nectar, pollen, resin or water. The oldest bees are conferred with the riskiest behavioural repertoires, involving foraging and nest guarding. If this scheme reflects optimal colony efficiency, then the actuarian statistics would indicate that each bee is most likely to 'repay' its social debt by first performing activities unlikely to result in early death. We discovered that the smallest colony of highly eusocial bee, *Melipona micheneri* (50 workers in a mature colony) has bees of all ages performing all tasks (T. Inoue and D. W. Roubik, unpublished). Flexibility is apparently necessary when the labour force is small. This social model appears best suited, among all bees studied, to mimic that occurring in human societies (Davis, 2009). Such societies exemplify hierarchy, specialisation, surplus and sedentary living. **See also**: Eusociality and Cooperation

Task allocation reflects the ability of multiple individuals to decide which activities are most pressing. The primary interest of the advanced social bees living in large colonies (thousands to tens of thousands of adults) is to know their queen well. Without pheromones, the glandular products with specific messages and responses in the insect brain and endocrine/nervous system, this would not be possible. 'Contact pheromones' are disseminated from the queen by her 'retinue' of worker attendants, and reach all portions of the nest and all individuals (Tautz, 2008). The brood area and its open cells (for honey bees) or closed cells (for meliponine bees), or chambers of multiple immature brood (allodapines and certain bombines) all contain and may disseminate pheromones that affect or regulate behaviour. When the queen dies, the colony must take action to rear another queen, or release a reserve queen from captivity. The former is the model for *Apis*, and the latter that of meliponines (see Michener, 1974). However, it is the gradual senescence and weakening of the queen that is registered in her vitality, rate of egg laying and the production of queen pheromones; it is not an 'all or nothing' regulation, thus shows a sophisticated grading of stimulus and response. **See also**: Chemical Ecology

Colony feedback as a mechanism for social regulation has been discussed extensively by Seeley (1995) and Tautz (2008) for Western hive bees, *A. mellifera*. If pollen is in short supply, more pollen foraging is encouraged, or if brood are too few, then new brood cells must be prepared and their production accelerated.

How did the Social Bees Evolve, and What Distinguishes their Colonies?

In biological theory on processes that produced social bees, there is a clear dichotomy. There are studies emphasising cooperation and reproductive harmony, and those that focus on conflicts between females. A feature that would ameliorate reproductive conflict is the single mating of the female, who produces females that are her helpers (Hughes *et al*., 2008). Hypotheses considering 'worker policing' and 'parent-offspring conflict' have guided research (Gadau and Fewell, 2009; Zimmermann *et al*., 2009; Schwarz *et al*., 2007), as well as the costs of inbreeding that lead to the production of sterile diploid males (Crozier and Pamilo, 1996). The next of kin to these paradigms is the parent of the scientific realm, which is 'kin selection theory' (Hamilton, 1964a, b; Trivers and Hare, 1976; Peters *et al*., 1999; Hughes *et al*., 2008). Prominent among the theoretical expectations are 1:1 sex ratios in colonies where a queen or reproductive dominant is in 'control', and a 3:1 bias in favour of females when the workers are 'trying hard' to produce personal offspring (Huth-Schwarz *et al*., 2011). (They cannot produce their own female offspring because they are sterile and unmated, but they can encourage production of colony offspring that contain their personal genetic lineage). **See also**: Eusociality and Cooperation; Natural Selection: Sex Ratio; Parent–Offspring and Sibling Conflict

Curiously, the unique role of honey for advanced social bees is practically ignored. At the pinnacle of social evolution, there is honey. Honey bees foraging for their colony collect and convert the nectar of millions of flowers averaging 40% sugar to honey having double this sweetness, and containing the simple sugars that they derive from sucrose–glucose and fructose. The meliponines do the same, but produce considerably less honey, which averages 30% water, but possesses flavours reminiscent of citrus, of higher acidity, and a variety of additional agreeable or potentially disagreeable qualities (Cortopassi-Laurino *et al*., 2006; Vit *et al*., in press).

To obtain the necessary resources to permit honey production, social and perennial colonies – stingless bees and honey bees – have evolved precise and effective communication to allow massive recruitment of nest mates to pollen, nectar and other resources. Their communication ability, expressed by returning foragers that emit sounds of different frequencies and intensities within the nest, in the midst of potential foraging bees seeking forage information, varies with species and genera. The honey bees communicate distance and direction, whereas some of the stingless bees either leave trails on vegetation or other substrates, or communicate height as well as distance and direction, using sounds within the nest. Although the honey bees are not aggressive foragers and very seldom skirmish with other foragers at flowering plants, certain stingless bees routinely mark resource patches with cephalic pheromones and then defend them vigorously.

To defend the large, perennial colonies and their stored brood, honey and pollen, colonies evolved advanced defensive behaviour, including stinging, biting and chemical defense. The larger and more advanced social colonies, those of *Apis* in particular, have evolved novel chemical components, distributed through the hollow tube of the sting, which cause pain, damage red blood cells, and envenomate vertebrates. Their nesting sites also are well protected, often having refuge underground, in fissures within rocks, or surrounded by several cm of living wood. There are many species, however, such as the smallest honey bees (*andreniformis* and *florea*) and nearly half of the stingless bees, which maintain a cryptic nest and use it to their advantage, lacking potent defensive mechanisms: although their sting hurts. They are timid, and after attack may abandon the nest (the honey bees) or retreat beyond the reach of natural enemies, and tightly seal off the nest entrance.

Honey has to be stored, because it is both necessary to refine nectar in a container and storage is honey's raison d'être. Honey is kept in wax vessels of two basic kinds. Wax is the very material that honey allows bees to produce. The cost of production is 7:1 (honey:wax) for *Apis* (Seeley, 1995), thereby promoting evolution of the most efficient energy storage among bees. The meliponines combine a similar amount of wax with resins from woody plants to make their honey 'pots' for food storage, all brood areas and other parts of the nest. By comparison, the pure wax nests of honey bees are monotonously uniform, but no less adapted to the bees. Further, the vertical combs of *Apis*, contrasted to the horizontal comb stacks, cell clusters, or single-sided vertical comb of a few stingless bees, provide a considerably greater range of temperature tolerance.

The honey bees make a vertical sheet of double-sided hexagonal cells, in which the cells have a slight upward slant. Brood of both castes and the males (drones) are placed in the same basic cells as nectar, honey or pollen. The entire comb is of pure wax, taken scale by scale from worker bees that extrude it from the wax gland slits on the underside of the abdomen. The scales are worked together and pressed into walls and sheets (the comb) by worker bees that manipulate the wax with their mandibles.

The honey bees and stingless bees have complementary methods of brood temperature and general nest regulation. Among the honey bees, adult workers can fill empty brood cells with their own bodies, fill the space between combs, and act as heat generators within the nest. This occurs in combination with blanketed layers of workers surrounding the outside comb, which slowly circulate to take honey for their own metabolism, and also enjoy warmth and protection in the centre of the nest. If outside environmental conditions are cooler than the ideal nest temperature – in the brood area where the queen lives – (approximately 30°C), bees increase their metabolism and radiate heat generated by gently 'flexing' the flight muscles. That heat is largely trapped by dense hair on the bees, but gradually dissipates. The stingless bees, in contrast, insert workers around brood layers, and generate heat to stabilise nest temperature. The brood area of many species able to inhabit cooler tropical regions is enveloped by sheaths of waxy building material, which also retards heat loss, and some chill tolerance exists (see Holcroft *et al.*, in Vit. *et al.*, in press). When it is too hot in the nest (above 45° is lethal), the meliponines fan their wings at the nest entrance and the inside corridor leading to it. By doing so, they are cooling their nest by convection of the high humidity in which the nest is encompassed, drawing out the warmer interior air and accomplishing some evaporative cooling at the same time.

Unlike meliponines, honey bees gather water from their environment and place small droplets on comb cell edges, then fan their wings to draw air across the water droplets and out of the nest. Both of these highly social groups must rid their nests of the water that evaporation from nectar produces. If fanning is inadequate, individual worker imbibe water from the nest interior and then fly from the nest to expel it. Their own metabolic water, and that from consumed nectar or honey, is gathered at latrines and either drained or carried from the nest. The dead bees and colony trash also are ejected.

How are Social Bee Populations Maintained?

The honey making bees depend on floral resources, and resin or water resources, within their flight range and area, which for a sedentary colony encompasses approximately 1–200 km^2. The honey bees use their considerable communication abilities not only to maintain their nesting colony. A reproductive or emigrating swarm uses the same mechanisms to establish which of the available nesting sites it will use. Much like foraging bees returning with information on the quality of a resource, the movements and sounds of bees that have assessed potential nesting sites impart critical information to bees in the resting swarm. These, based on the number of favourable reports coming back to their bivouac, decide whether to fly to a new nest site and occupy it, or to move on to another area, and repeat the search for a new home base. Nest qualities such as total protected volume are physically measured by worker bees walking within them, and serve as a principal basis for rejecting or accepting a new nesting site. Some of the giant honey bee species, such as *A. dorsata* and *A. laboriosa*, spend a portion of the year with no wax comb and sometimes with no fixed nest site. In addition, both species have regional populations with few or no migratory colonies (those that depart and return during different parts of the year, largely in unison), as well as populations that seem to migrate completely, within each year.

Meliponines, just like the honey bees, reproduce by colony 'fission', but do so very infrequently, perhaps only twice each 20 years (Roubik, 2006). Their nesting sites and number of individual colonies are, in most natural situations, extraordinarily limited (Kajobe and Roubik, 2006). A fundamental difference between the honey bees and stingless bee is that the former are free-swarming. A colony issues from a mother nest, with the established queen at its head, and the nesting site is relinquished to a new queen and a portion of the worker population. In contrast, meliponines have an important restriction. They require a new nest to be fully prepared, with a carefully made entrance and some stored food, before a new queen (that being unmated, can still fly) and a portion of the mother colony's workers, can fly directly to it. Its distance from the parent colony cannot exceed a few 100 m. In some instances, the mother colony continues to support a daughter colony after it separates, by allowing workers to carry food or building material from one nest to the other.

The honey bees reproduce during the active season of the most intense flowering, as do the stingless bees, and thereby replace those colonies lost to starvation or predation. There are documented declines in some bumble bees and honey bees (*A. mellifera*) in the UK, Europe and the United States, presumably due to habitat destruction, or implicated pathogens and insecticides (Potts *et al.*, 2011; Cameron *et al.*, 2011; Hagen *et al.*, 2011; Brittain and Potts, 2011). Because both *Apis* and *Bombus* forage widely (see Hagen *et al.*, 2011) and use many species of flowering plants, they may be adequate monitors of general environmental quality for bees. However, highly social bees mix different sources of nectar together and also combine several types of pollen in their food stores, which dilutes any one source of inferior nutrition or environmental toxin. On the other hand, the colonies of *Apis* utilise over 200 km^2 of foraging area, and some of their best known and widely distributed species are migratory, thus use even broader portions of different environments (Roubik, 1989). Migratory behaviour in tropical *Apis dorsata* and *A. mellifera* is normal (see Oldroyd and Wongsiri, 2006), thus corridors that extend from their origins to alternative sites are important. However, many other social and solitary bees are firmly rooted where they live, and may rely heavily on a few plant species or other resources, close by and in a defined season.

The distribution of nests, that is, the number found within a square km, is in some species highly predictable or regulated by aggressive interactions between colonies (summaries in Roubik, 1989, 2006). Hence, the future of this single largest advanced social group depends on complex and yet unstudied factors, including perhaps diversity of pests, parasites, resources, competitors and mutualists, and human influence. Because such bee colonies can be propagated and fed in hives (Nogueira-Neto, 1996) and humans can certainly plant gardens or other areas to promote 'bee flowers' (Cane, 2011) certain human influence can clearly be positive.

Bumble bees and the perennial colonies of honey bees and meliponines in particular, are likely to use more floral species than do solitary bees, even though the single long-term study of solitary bees in the tropics shows that they, too, use many different species (Roubik and Villanueva, 2009). To keep records of floral species use, bee abundance and determine how behaviour and ecology change, with future changes in the world's environments, should be one clear priority for the understanding of social bees and their ecology. **See also**: Climate Change Impacts: Insects

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