

Comparative methods offer powerful insights into social evolution in bees

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Abstract – Bees are excellent models for studying the evolution of sociality. While most species are solitary, many form social groups. The most complex form of social behavior, eusociality, has arisen independently four times within the bees. Subsequent elaborations of the reproductive division of labor inherent to eusociality have led to the evolution of some of the most highly advanced forms of eusociality documented. Likewise, many reversals back to solitary behavior also create substantial variation in sociality within the bees. These replicated, independent origins and losses enable a comparative approach that facilitates the search for common mechanisms underlying transitions from solitary to group living. In this review, we discuss the extensive behavioral variation found within the bees and highlight how the comparative method has improved our understanding of social evolution. Finally, we discuss potential difficulties with this approach and outline promising avenues for future research.

comparative method / evolution / communal / semisocial / eusocial / genetics / genomics

1. INTRODUCTION

The study of social evolution comprises two central questions: the first concerned with the origins of social behavior and the second with its maintenance in social groups. An understanding of the factors associated with the origins and losses of sociality requires a comparative approach that examines evolutionary transitions in social behavior throughout the phylogeny, while studies of single species can greatly inform our understanding of some of the processes maintaining social traits such as

reproductive division of labor. In this review, we focus on understanding the first of these questions: the evolutionary origins of sociality. We argue that comparative methods can greatly inform our understanding of both proximate mechanisms and ultimate causes of social behavior, and that bees are an ideal group for these types of studies.

Though social behavior occurs in a wide variety of contexts when two conspecific animals interact, in the context of social evolution its use is more often restricted to the cooperative, non-agonistic and non-sexual interactions among conspecifics sharing a common nest in which offspring are reared. Defining sociality in this way encourages us to address questions of why and how animals form cooperative groups. Though social group formation may bring benefits to individuals and have many underly-

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ing explanations, social behavior often entails forfeiting of personal reproduction. It is this individual altruism associated with cooperative group formation that has been viewed as an evolutionary paradox.

Eusociality is arguably the most derived form of social behavior with behaviorally discrete reproductive castes (i.e., forfeiting of reproduction by workers but not queens), and has held special prominence among evolutionary biologists because it represents one of the major transitions of life: from a solitary lifestyle to a coordinated group cooperating to reproduce (Maynard Smith and Szathmari 1997). Inclusive fitness remains the central theoretical paradigm for understanding social evolution and the transition to eusociality (Hamilton 1964; cf. Nowak et al. 2010).

Though eusociality is taxonomically rare (ca. 2 % of insect species are eusocial, Wilson 1990), organisms that have achieved this higher level of organization frequently meet great ecological success, with eusocial species representing approximately 50 % of the world's insect biomass (Wilson 1971). Eusociality has been best described in the insect order Hymenoptera, and especially in the bees where multiple origins of eusociality have occurred independently (Figure 1). For this reason, bees are excellent models for studying social evolution within a comparative context.

Here we present an overview of social diversity in bees, explore how a comparative approach has aided our understanding of the why and how of social evolution, and then discuss current problems in this approach and promising directions for future research.

1.1. Diversity of social behavior in bees

Social behavior is commonly categorized into six major social types: solitary (lacking social behavior), subsocial (those with extended parental care), communal, semisocial, quasisocial (the latter three collectively called parasocial), and eusocial (Table I). The term 'eusocial' was first proposed by Susan Batra to describe the social behavior of some halictine bees (Batra 1966b). Wilson (1971) expanded the definition of eusoci-

ality to describe all societies with three main characteristics: overlapping generations, cooperative brood care, and a reproductive division of labor with effectively sterile worker castes. Michener (1974) further subdivided eusociality into 'primitive' and 'advanced'. These terms were designed to emphasize the differences among types of eusocial societies: those with high degrees of morphological differentiation between queens and workers ('advanced', e.g., *Apis mellifera*), and those with less clearly differentiated castes based primarily on size ('primitive', e.g., paper wasps or halictid bees). The many forms of social behavior that have evolved within bees arguably reflect greater social lability than in any other group in the Hymenoptera (Table II).

Many species of solitary bee nest in aggregations where each female constructs her own nest in close proximity to other females' nests. This leads to the grouping of nests into an aggregation, and is often characteristic of many ground nesting bees, including members of most of the major bee families/subfamilies: Andrenidae, Apidae (including the Anthophorinae and the Apinae), Colletidae, Halictidae, and Mellitidae (Knerer and Plateaux-Quenu 1966; Wilson 1971; Michener 1974; Stark 1992; Plateaux-Quenu 1993a; Rehan et al. 2010). One explanation for aggregated nesting may be limited distribution of suitable substrate in which to construct a nest; another is hypothesized to be defense against parasites through the selfish herd, though the data are equivocal on this point (Batra 1966b; Michener 1969; Wilson 1971; Rosenheim 1990). While not strictly social, aggregated nesting requires tolerance of neighbors as well as recognition of own versus conspecific nests, traits that may be precursors to the highly cooperative behavior and refined nestmate discrimination abilities described in eusocial bees (Michener 1974; Spessa et al. 2000; Nowak et al. 2010; Cardinal and Danforth 2011).

Parasocial colonies, consisting of adults generally from a single generation, have been described extensively in the bees. One example of a parasocial lifestyle, communal nesting, occurs when a number of females provision and lay their own eggs (e.g., without castes) in a

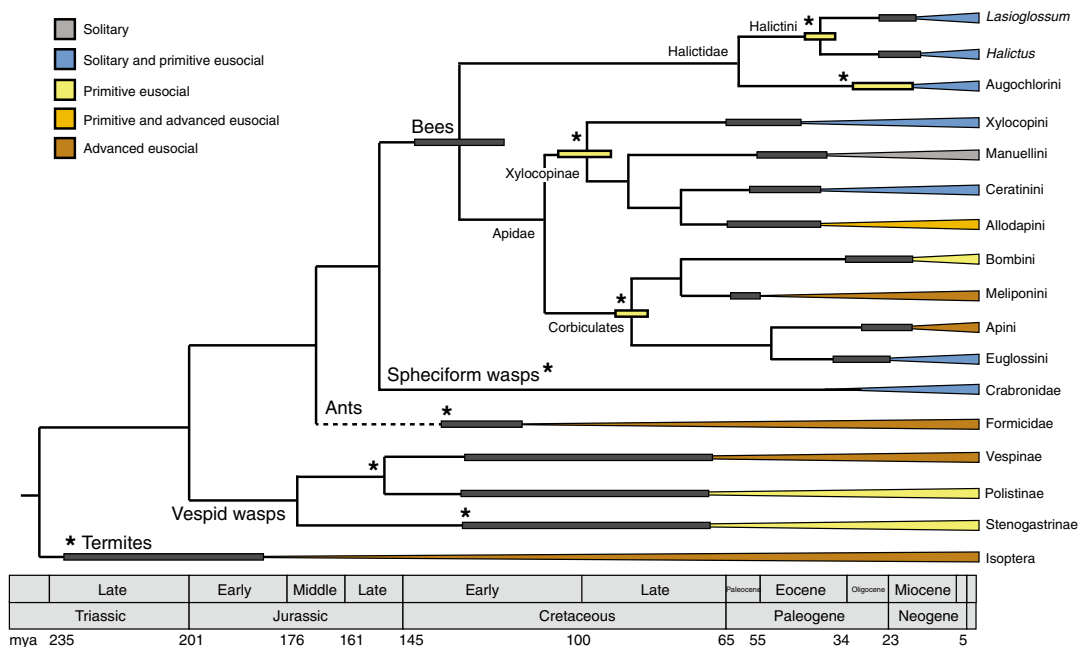


Figure 1. The evolution of major eusocial, extant clades in bees, other Hymenoptera and Isoptera (termites). Clades not shown are solitary or parasocial. Asterisks indicate independent origins of primitive eusociality. Colors indicate the forms of sociality that occur within each group and the lengths of the bars indicate the temporal range at which each gain or loss has been estimated. Dates and references are documented in Table II.

shared nest. Communality is taxonomically widespread, and has been documented in the Mellitidae, Halictidae, Andrenidae, Apidae, Colletidae, and Megachilidae. Other types of parasocial behavior have also been characterized, such as associations between multiple females during the breeding season with some degree of reproductive division of labor (Knerer and Plateaux-Quenu 1966; Batra 1966a; Stark 1992; Plateaux-Quenu 1993a; Ulrich et al. 2009; Rehan et al. 2010). Parasocial associations have been documented in several tribes within Apidae (Xylocopini, Allodapini, Ceratinini, and Euglossini), Halictidae (Halictinae), and Colletidae (Hyalinae) (Spessa et al. 2000; Cardinal and Danforth 2011; Danforth et al. 2013). Often these interactions involve cooperative founding of nests by two or more females (e.g., *Halictus scabiosae*, Batra 1966a; Wilson and Holldobler 2005; Ulrich et al. 2009), or a division of labor where some females guard the nest while

others forage and lay eggs (e.g., Xylocopini/*Xylocopa sulcatipes*, Stark 1992; Schwarz et al. 2011; Ceratinini/*Ceratina* spp., Rehan et al. 2009).

Only a small proportion of bee species (ca. 6 %, Danforth 2007) are eusocial with a clear division of labor established and maintained by one or a few reproductive individuals (Figure 1; Table II). Unlike the parasocial colonies described above, eusocial nests consist of distinguishable reproductive castes that cooperate in brood care. These castes are composed of adult individuals from two overlapping generations that are both potentially able to reproduce (typically mothers and daughters).

Some lineages, such as the honey bees and stingless bees, represent highly derived forms of eusociality where large colony sizes, morphological caste dimorphism, and a developmentally determined reproductive division of labor are well established. Based on the current phylogeny, no reversals to a solitary life history can be

Table 1. Definitions of social behavior in the literature.

	Alloparental care	Reproductive division of labor	Overlapping adult generations	Further descriptors	References
Solitary	–	–	–	May nest in aggregations	Michener 1969
Subsocial	–	–	–	Extended parental care	Michener 1969
Parasocial					
<i>Communal</i>	–	–	–	Females share nesting area	Michener 1969
<i>Quasisocial</i>	+	–	±		Michener 1969
<i>Semisocial</i>	+	+	–		Michener 1969
Social	+	–	–	Any group living species with “reciprocal communication of a cooperative nature”	Costa & Fitzgerald 1996; Wilson 1971
Eusocial					
<i>Primitively eusocial</i>	+	+	+	Reproductive and non-reproductive castes are morphologically indistinguishable	Michener 1969
				Workers typically capable of mating	Wilson 1971
<i>Advanced or highly eusocial</i>	+	+	+	High degree of morphological variation between castes	Michener 1969
				Workers typically incapable of mating	Wilson 1971
<i>Facultatively eusocial</i>	+	+	+	The reproductive caste is totipotent and/or capable of surviving on its own	Crespi & Yanega 1995
<i>Obligately eusocial</i>	+	+	+	Both castes are mutually dependent on each other	Crespi & Yanega 1995

Modified from Michener (1974)

inferred among these extant, highly eusocial lineages (Schwarz et al. 2007). This suggests that these species may have crossed an evolutionary ‘point of no return’ (Wilson and Holldobler 2005) which may entail the loss of reproductive capabilities in workers.

Other bee lineages, such as halictids and xylocopines, have seemingly less-derived forms of eusocial behavior with smaller colony sizes. Colonies are often annual and founded solitarily by the queen: they become eusocial as their ontogenetic end-point. These species lack (or have lower levels of) morphological caste dimorphism, and workers have the ability to mate and lay fertilized,

female-destined eggs. In halictids and xylocopines, reversions from eusociality back to solitary life histories are widespread. This often results in a great deal of variation in social structure within and between species (Figure 1; e.g., Halictinae and Xylocopinae, Wcislo and Danforth 1997; Schwarz et al. 2007). Allodapines, in contrast, seem not to exhibit reversions to a solitary lifestyle (Chenoweth et al. 2007).

Based on our current understanding of the phylogenetic relationships within the bees, eusociality appears to have arisen four times independently (twice in Apidae and twice in Halictidae) with many subsequent modifications

Table II. The evolution of major eusocial clades.

Group	Clade	Social transition	N (Eusocial)	Est. date	Range	Geological period	Reference
Bees	Corbiculates*	<i>Solitary</i>	711	87	78–95	Late Cretaceous	Cardinal & Danforth 2011
	Apini	<i>Primitive</i>	11	22	16–30	Oligocene–Miocene	Cardinal & Danforth 2010
	Meliponini	<i>Primitive</i>	500	58	56–61	Early Eocene	Cardinal & Danforth 2011
	Bombini	<i>Primitive</i>	200	21	12–31	Oligocene–Miocene	Cardinal & Danforth 2011
	Euglossini	<i>Primitive</i>	0	28	21–35	Oligocene–Miocene	Cardinal & Danforth 2011
	Xylocopinae*	<i>Solitary</i>	253+	99	89–111	Late Cretaceous	Rehan et al. 2012
	Allodapini	<i>Primitive</i>	250+	53	45–59	Paleocene–Eocene	Rehan et al. 2012
	Ceratinini	<i>Primitive</i>	3–4?	51	43–57	Paleocene–Eocene	Rehan et al. 2012
	Manuellini	<i>Primitive</i>	0	46	39–54	Paleocene–Eocene	Rehan et al. 2012
	Xylocopini	<i>Primitive</i>	0	50	42–62	Paleocene–Eocene	Rehan et al. 2012
Apoid Wasps	Halicini*	<i>Solitary</i>	300+	35	38–43	Oligocene–Miocene	Brady et al. 2006; Gibbs et al. 2012
	Augochlorini*	<i>Solitary</i>	25+	20	12–29	Oligocene–Miocene	Brady et al. 2006
	Crabronidae	<i>Solitary</i>	50	–	–	–	Wenzel and Pickering 1991; Ross & Matthews 1991
	Polistinae + Vespinae	<i>Solitary</i>	880	>65	–	–	Wenzel and Pickering 1991; Hines et al. 2007
	Stenogastrinae	<i>Solitary</i>	–	>65	–	–	Wenzel and Pickering 1991; Hines et al. 2007
Ants	Formicidae	<i>Solitary</i>	11,000	120	115–135	Early Cretaceous	Brady et al. 2006; Johnson et al. 2013
	Isoptera	<i>Solitary</i>	2,200	200	180–230	Late Triassic–Early Jurassic	Ware 2010
Thrips	Thysanoptera	<i>Solitary</i>	6	6.32	5.25–9.36	Miocene–Pliocene	McLeish & Chapman 2007
Aphids	Homoptera ^c	<i>Solitary</i>	60	–	–	–	Pike & Foster 2008
Ambrosia beetles	Platypodinae	<i>Solitary</i>	2	–	–	–	Kent & Simpson 1992; Biedermann & Taborsky 2011

Asterisks indicated independent origins of eusociality within the bees. Note that the ‘social transition’ column represents the most extreme forms of sociality found within the group. Although definitions do not allow us to expand on what we see as a transition to a more sophisticated form of eusociality in *Bombus*, social behavior in this group includes a number of traits often associated with ‘advanced’ eusociality, including the production of queen pheromones, occasional swarm founding, thermoregulation, and coordinated foraging by workers.

^b Some morphological specialization among castes appears to have occurred at least once (and perhaps twice) in allodapine species (Schwarz et al. 2007)

^c It is possible that eusociality has evolved independently within the aphids up to 17 times (Pike and Foster 2008)

(Table II; Figure 1). The evolution of complex or so-called advanced eusocial behavior occurred twice in the corbiculates (in Apini and Meliponini) and perhaps once in the Allodapini, where at least one species shows signatures of morphological caste specialization (see below for discussion of definitions; Brady et al. 2006; Cardinal and Danforth 2011; Rehan et al. 2012; Gibbs et al. 2012).

The role, if any, of communality in the evolution of eusociality remains unclear. The current view is that communality represents an evolutionary dead-end (Paxton et al. 1996; Tierney et al. 2008), yet given the widespread taxonomic distribution of communality, many eusocial lineages also appear to harbor communal taxa within the same clade as either a derived or ancestral state. However, there are many lineages with solitary and communal species but lacking eusocial species (Michener 1974), suggesting that communal behavior is not sufficient for the transition to eusociality. Behavioral data on additional species sister to eusocial lineages will help to reveal the evolutionary origins of communality. If communality is ancestral to eusocial species, this would suggest that communal behavior represents a pre-adaptation to eusociality rather than simply a behavioral side road and stable end-state of social organization. The role, if any, of other forms of parasocial organization in the evolution of eusociality is even less clear because of a paucity of data.

1.2. Comparative methods and the search for mechanism

The comparative method as a means of hypothesis testing in biology was statistically formalized in the 1970s to help interpret variation in social and sexual behavior among vertebrates, particularly primates (for review, see Davies et al. 2012). These early studies searched for statistical associations between one or more traits and social organization (e.g., the relationship between canine length in male primates and social group structure, Harvey et al. 1978). Though accounting for allometric relationships within the data, these early

approaches attempted to account for phylogenetic non-independence using an ad hoc approach: by undertaking analyses at various taxonomic levels (e.g., species, genus, and family). Subsequently, these methods have been refined to better account for phylogenetic non-independence using a robust statistical framework well suited to hypothesis-testing in which traits are mapped directly onto a phylogeny that is generated independently of those traits, usually using DNA sequence data (e.g., phylogenetically independent contrasts, see Harvey and Pagel 1991; phylogenetic generalized least squares models, see Grafen 1989). These methods can be used to test for associations among traits while explicitly controlling for phylogenetic relationships (e.g., cooperative breeding in birds, Székely et al. 2013).

The repeated gains and losses of sociality in bees make them an ideal system for using comparative methods to study the evolution of social behavior. The multiple independent origins and subsequent reversals represent independent replicates that can be used to test hypotheses related to both proximate mechanisms and ultimate factors favoring transitions in sociality. Our current understanding regarding the number of origins of sociality and transitions among social forms are based on a rigorous analysis of bee phylogenies onto which social traits have been mapped. Furthermore, the phylogeny of bees is relatively well resolved (Danforth et al. 2013), creating a statistically robust framework in which to conduct these tests.

One particular group of bees, the halictids, has been the focus of many comparative studies. Two of the four origins of sociality in bees occur within this group. Coupled with many subsequent losses, this has resulted in a vast amount of variation in social behavior among closely related species. This variation is even known to occur within single species, with females of these taxa exhibiting both eusocial and secondarily solitary behavior (*Augochlorella aurata*, Packer 1990; *Halictus rubicundus*, Yanega 1988; Eickwort et al. 1996; *Lasioglossum albipes*, Plateaux-Quenu 1993b; Plateaux-Quenu et al. 2000; *Lasioglossum baleicum*, Cronin and Hirata 2003; *Lasioglossum calceatum*, Sakagami and Munakata 1972;

Megalopta genalis, Wcislo et al. 2004). In this group, comparative approaches have identified a number of factors that appear to be associated with eusociality, including: the proportion of females in the first brood, proportion of unmated workers, proportion of workers with undeveloped ovaries, mean number of workers per colony, increased contact between adults and developing brood, and size dimorphism between queens and workers (Breed 1976; Packer and Knerer 1985; Packer 1991).

1.2.1. Comparative ecological approaches

A number of ecological factors have been proposed as selective forces favoring social living not only in bees but also in a range of other social taxa. Directly or indirectly, these ecological factors relate to reduced dispersal, improved defense against parasites (interspecific and intraspecific), facilitation of nest construction, and provisioning of offspring as routes to enhanced reproductive output of a nest. Within the inclusive fitness framework of Hamilton (1964), these contribute to the benefit (b) and cost (c) variables of Hamilton's rule ($rb/c > 1$). Though many of these ecological factors have been examined in only one or a few species thus far, we feel that a discussion of these factors is critical to our understanding of the evolution of sociality and hope to encourage future work that examines their role in a comparative framework when possible.

Variation in sociality with respect to geographic patterns may give hints at some of the relevant ecological factors, and many such patterns have been documented in recent years, though the overall picture is not clear. Several studies have identified gradients of sociality that seem to be associated with altitudinal and latitudinal clines (reviewed in Purcell 2011). In most cases, species exhibit higher degrees of sociality at lower altitudes and latitudes. For example, many halictid bee species do not produce workers at high altitudes and latitudes (e.g., *H. rubicundus*, Yanega 1988; Soucy and Danforth 2002; Soro et al. 2010; *A. aurata*, Packer 1990; *L. baleicum*, Yanega 1988; Cronin

and Hirata 2003; *L. calceatum*, Sakagami and Munakata 1972). However, some taxa show the opposite pattern, with greater caste differentiation occurring at higher altitudes and latitudes (e.g., *H. ligatus*, Richards and Packer 1996). In addition, the proportion of social species in bee communities tends to increase at high elevations (Hoiss et al. 2012). Similarly, in *Bombus*, queen-worker caste dimorphism and the number of first-brood workers tends to increase at higher latitudes (Lavery and Plowright 1985). Furthermore, in the ants, species in 17 out of 19 genera and five out of six subfamilies tend to have larger colony sizes at high latitudes (Kaspari and Vargo 1995, but see Purcell 2011). Future work examining the distribution of solitary and social species across environmental gradients could greatly illuminate our understanding of how and why different taxa appear to respond in opposite ways to these environmental variables.

Importantly, altitude and latitude also correlate with many ecological variables, including: climate, predation, resource availability, and parasites and pathogens. These factors may also help to explain the variation in social behavior across these physical gradients as well as differences among species in these patterns. However, disentangling their relative importance remains a challenge (see Bourke 2011; Purcell 2011 for recent reviews). For example, temperature is strongly correlated with altitude and latitude, with shorter growing seasons found at higher elevations and latitudes. Shorter growing seasons can limit the amount of time available for social species to produce worker and reproductive broods, and may be associated with shifts to alternative life histories in regions with shorter seasons (e.g., social parasitism in *Bombus (Alpinobombus) hyperboreus*, Alford 1975; reversions to solitary behavior in halictids, Sakagami and Munakata 1972; Yanega 1988; Packer 1990; Soucy and Danforth 2002; Cronin and Hirata 2003; Soro et al. 2010). In regions with shorter growing seasons, there may simply be insufficient time to complete the production of a worker and a sexual brood.

Alternatively, environmental variability might select for group life as a way to buffer against harsh or extreme periods, just as it selects for extended parental care in insects in general (Wong et al. 2013). In some ant, termite, and social spider species, rainfall is positively correlated with sociality (Riechert et al. 1986; Picker et al. 2007; Murphy and Breed 2007; Purcell 2011). However, the highly eusocial allodapine bee species *Exoneurella tridentata*, appears to have evolved sociality in very harsh, xeric conditions (Dew et al. 2011), and in years with harsh weather conditions colonies of *H. ligatus* showed an increase in sociality (i.e., higher levels of queen-worker dimorphism and decreased worker cheating; Richards and Packer 1996). In a similar vein, communality among the bees may also be associated with more arid environments (Australia, SW USA) because of restricted opportunities for fossorial nesting (Wcislo and Tierney 2009), though more rigorous comparative studies are needed to support this view. Similar patterns have also been documented in social vertebrates. In mole-rats, the degree of sociality increases as resource abundance decreases and variability in rainfall increases (Faulkes et al. 1997; O'Riain and Faulkes 2008). Furthermore, cooperative breeding increases in African starling taxa that are associated with semi-arid environments and/or with high variability in rainfall (Rubenstein and Lovette 2007). Associations can also be examined by searching for a correlation between sociality and each of these environmental factors (e.g., rainfall, environmental variability, etc.) while explicitly controlling for phylogenetic signal (as in Rubenstein and Lovette 2007).

Variability in resource abundance may also favor non-dispersal and increased group sizes (Stacey and Ligon 1991). Evidence for this comes from social vertebrates where experimental manipulation of food resources can lead to an increase in cooperative breeding in carrion crows (Baglione et al. 2006). In Seychelles warblers, an increase in helping is observed when nests occur in a territory where food resources are high and vacant territories are of low quality (Komdeur 1992). The corollary of resource abundance is habitat saturation, which may also

play a role in favoring sociality. For example, low availability of vacant nesting sites or territories can select for non-dispersal (Emlen 1982). This has been documented in allodapine bees where *Exoneura nigrescens* females remain in their natal nests at higher frequencies when additional nesting sites are experimentally removed (Langer et al. 2004); but see Bull and Schwarz 1996 for an opposing result in *Exoneura bicolor*.

Pressures from parasites and predators have also been proposed to favor social groups because groups are thought to be better protected from both heterospecifics (Lin and Michener 1972; Evans 1977) and conspecifics (cheaters). *Xylocopa suclatipes* is a socially polymorphic species with a proportion of nests containing a secondary female that guards the nest; the presence of the guard bee significantly reduced the frequency of nest usurpation by a conspecific female when the habitat was saturated (limited nest-site availability; Stark 1992).

Finally, group living may increase foraging efficiency or it may increase the predictability of available resources because multiple foragers can decrease the variance in the amount of food gathered on a daily basis (Wenzel and Pickering 1991; Stevens et al. 2007). This latter idea, encapsulated in the Central Limit Theorem (Gillespie 1977), may further help to buffer the colony against harsh and/or variable environments and also divides the foraging load over a number of individuals, perhaps reducing the cost of foraging for any single female. The only direct test of this hypothesis for a bee species that straddles the sociality spectrum, *H. rubicundus*, supports the idea that solitary mothers invest more in foraging than social mothers (Field et al. 2012) but does not explicitly address variance in resource income in social versus solitary nests.

Importantly, life history traits often interact directly with ecological factors, and some of these might serve as pre-adaptations to the evolution of eusociality (Andersson 1984). These include traits such as having a nest to defend and an increased dependence of offspring on parents (e.g., progressive provisioning). At a very simplistic level, short adult lifespan coupled with long juvenile development is likely to constrain the evolution of

sociality because it limits the opportunity for mother and daughter to overlap. Extended lifespan of an adult sweat bee foundress over two winters may lead to a eusocial nest in otherwise solitary species (e.g., *Lasioglossum fratellum*, Field 1996). Extended offspring dependence on adult provisioning or protection can, however, favor group living through assured fitness returns (Gadagkar 1990), as seen in hover wasps (Field et al. 2000), halictid bees (Smith et al. 2003), and allodapine bees (Schwarz et al. 2011). Assured fitness returns may also favor the transition to sociality in bees, though we know of no direct tests for its role in this group.

Clearly much more work is needed to assess differences among solitary and social species to determine if these geographical and ecological patterns are strongly correlated with sociality. We have highlighted a number of factors thought to play a role in the evolution of social behavior, and pointed to areas of research where comparative methods can be employed to search for these associations while controlling for phylogeny. More studies examining these factors in additional bee species are necessary in order to facilitate these comparisons. Finally, mapping of life history traits considered to be pre-adaptations to sociality onto the current phylogeny will help to determine which, if any, of these traits correlate with social behavior after explicitly controlling for phylogenetic relationships. Furthermore, recent advances in comparative phylogenetic methods, particularly in Bayesian analytical techniques, now allow users to account for phylogenetic uncertainty, making these tests more robust and applicable to a wide range of species (Pagel and Meade 2006, 2013).

1.2.2. Comparative genomic approaches

Our understanding of some of the ultimate factors associated with the evolution of social behavior has improved greatly over the past 50 years. Kin and multilevel selection theory can, at least in part, explain the persistence of a sterile worker caste in highly eusocial insect societies, using either an inclusive fitness or

population genetic perspective, respectively. However, we still lack a clear understanding of the proximate genetic mechanisms underlying social behavior.

Comparative genomic methods can improve our understanding of some of these genetic mechanisms. However, it must be emphasized that most of these approaches operate on the assumption that there is a common genetic toolkit underlying reproductive division of labor in social insects (Toth and Robinson 2007). For example, the reproductive ground plan hypothesis posits that the molecular pathways associated with nest founding and offspring provisioning in a solitary ancestor were coopted to establish the division of labor in eusocial societies (West-Eberhard 2003).

Current evidence indicates that this may indeed be the case. ‘Functional’ genomic approaches have compared differences in gene expression associated with task specialization between nurse and forager worker honey bees to differences in gene expression between foundresses and established queens in paper wasp females (Toth and Robinson 2007; Toth et al. 2007; Toth et al. 2010). These results suggest that the molecular pathways associated with task specialization in honey bees have indeed evolved from ancestral Hymenoptera gene networks associated with nest founding and brood care. Further evidence comes from the examination of juvenile hormone (JH) in the facultatively eusocial halictid, *Megalopta genalis* (Wcislo et al. 2004; Smith et al. 2012). JH is associated with ovarian development in solitary insects but with dominance status and reproductive division of labor in social insects, leading to the prediction that JH might represent a mechanism for decoupling reproduction and parental care (West-Eberhard 2003). Measurements of juvenile hormone in reproductive and non-reproductive *M. genalis* females suggest that this may indeed be the case (Smith et al. 2012). However, transcriptomic approaches in *Polistes canadensis* and in several ant species have also suggested that reproductive division of labor might be associated with the evolution of novel genes (Gadua et al. 2012; Ferreira et al. 2013).

Importantly, all of these analyses rely on a comparative approach to search across species for common molecular pathways underpinning caste differentiation. Somewhat surprisingly, convergent molecular evolution may be more commonplace than one might initially suspect. A recent study examining the convergent evolution of echolocation in bats and cetaceans identified hundreds of loci where similar changes occurred at the amino acid level (Parker et al. 2013). These results suggest that the genetic underpinnings associated with convergent, independently evolved phenotypes may often be the same.

A similar approach can be used to search for the molecular underpinnings of caste differentiation in social insects—examination of a large number of social insect taxa within a clear phylogenetic framework will likely inform our understanding of some of the proximate mechanisms underlying social evolution. For example, comparative genomic approaches that examine the genomes of multiple solitary and social species can be used to search for signatures of selection on protein coding genes that are shared within behavioral forms. This type of approach was first utilized in bees by comparing expressed-sequence tag (EST) data from 11 different bee species, where genes associated with chemical signaling, metabolism, brain development, and immunity showed signatures of positive selection in species with both primitive and advanced eusociality (Woodard et al. 2011; Fischman et al. 2011). Future work could compare closely related social and solitary taxa to determine if there are genes or gene networks unique to eusocial taxa that are missing in solitary ones and that might represent a ‘point of no return’ to eusociality.

The type of genomic data required for comparative analyses is highly dependent on the types of questions one is interested in addressing. For example, in a search for common pathways underlying the evolution of eusociality, transcriptomic data is sufficient because current tests for selection use the ratio of synonymous vs. non-synonymous mutations as evidence for selection—an excess of non-synonymous (e.g., amino acid) mutations suggests that there has been strong positive selection on those loci (Yang

and Bielawski 2000). Therefore, coding sequences are all that is needed for this level of comparison. However, *de novo* transcriptome assembly remains challenging, and whole genome assemblies can greatly improve gene annotation, particularly with respect to paralogous sequences (Vijay et al. 2013). Furthermore, for questions related to the evolution of genome structure (e.g., transposable elements, repetitive sequences, or whole genome duplications), whole-genome sequences are essential.

2. CURRENT CHALLENGES

2.1. Defining eusociality

One of the major limitations of employing a comparative approach to study the evolution of social behavior is a clear definition of the behavioral forms being studied. Numerous proposals to improve the definitions in Table I have been made over the years (Crespi and Yanega 1995; Sherman et al. 1995; Costa and Fitzgerald 1996). Crespi and Yanega (1995) argued for a more restricted definition of eusociality to include only species where castes become “irreversibly behaviorally distinct at some point prior to reproductive maturity”. Conversely, Sherman et al. (1995) argued that the definition of ‘eusocial’ should be expanded to encompass all species with “alloparental helping of kin”. Despite disagreements on the broader framework, both advocated abandonment of the terms ‘primitive’ and ‘advanced’ eusocial. Crespi and Yanega suggested two alternative terms, facultative and obligate eusociality, meant to de-emphasize the ‘value-laden’ nature of ‘primitive’ and ‘advanced’. Rather than leading to a consensus in the field, these efforts appear to have resulted in additional confusion, with different research teams adopting different terminologies to describe the same or very similar species (Costa and Fitzgerald 2005; Lacey and Sherman 2005).

At a time when comparative phylogenetic and genomic methods are meeting increasing success, the limitations of these terms and reluctance in the field to develop standardized definitions of existing terms is a major limitation. The categorical nature

of these terms coupled with lack of consensus in their definitions impedes the use of comparative methods to search for common factors associated with variation in social behavior. For example, bumble bees are often called ‘primitively eusocial’ because the only morphological difference between a queen and a worker is size (Michener 1974). However, this term has been described as “misleading” (Goulson 2003) because bumble bees can regulate temperatures within the nest (Heinrich 1979), communicate the presence of floral resources to other colony members (Dornhaus and Chittka 2001; Dornhaus et al. 2003), workers are generally not known to mate (Heinrich 1979; Goulson 2003), and at least one *Bombus* species can found new colonies via swarming (Garófalo 1974) in manners akin to the ‘advanced’ honey bees and stingless bees. Because bumble bees are technically deemed primitively eusocial, they are often included in the same behavioral groups as halictid bees and polistine wasps (e.g., Woodard et al. 2011), which have lesser size differentiation between queens and workers, much smaller colonies, and cannot effectively thermoregulate their nests.

Sociality is more likely to be a continuous rather than discrete character, and finer-scale quantification could provide better resolution in the search for genetic, behavioral and ecological factors underlying the evolution of social groups. Indeed, some attempts have been made to develop quantitative indices to characterize gross differences in sociality across a wide array of taxa. In order to maximize inclusivity, they focus primarily on reproductive skew (Sherman et al. 1995) or the energetic contribution of workers (Keller and Perrin 1995). More recently, these indices have been expanded to include measures of dispersal (Avilés and Harwood 2012). However, common measurements for these terms have not been adopted across fields, and often include different assumptions that are not directly comparable (Nonacs 2000).

2.2. Correct phylogenies

The comparative method explicitly relies on the evolutionary relationships of organisms to

search for commonalities across species. Therefore, it is critical that the phylogenetic relationships within a group of interest are well characterized. Fortunately, in recent years, the publication of several molecular phylogenies of bees (Brady et al. 2006; Cardinal and Danforth 2011; Rehan et al. 2012; Gibbs et al. 2012), wasps (Hines et al. 2007) and ants (Brady et al. 2006; Moreau et al. 2006) has substantially improved our understanding of these relationships within the Hymenoptera. These phylogenies are poised to facilitate comparative studies of a number of traits associated with eusociality (reviewed in Danforth et al. 2013).

Good phylogenies aside, when evaluating a phylogeny there are a number of factors that must be considered. For example, the loci used to construct the tree can influence topology. Ideally, a combination of nuclear and mitochondrial genes should be used to reconstruct evolutionary relationships because mitochondrial loci have matrilineal inheritance patterns, which can sometimes obscure the evolutionary history of the focal taxa. More recent datasets incorporate multiple loci using genome-wide data to resolve these phylogenies (Song et al. 2012). In these instances, the ‘gene trees’ are not always consistent, and this discordance needs to be accounted for when inferring evolutionary relationships (Degnan and Rosenberg 2008). Fortunately, recent developments in Bayesian analytical techniques, such as those in BayesTraits, are now able to encompass phylogenetic uncertainty (Pagel and Meade 2006, 2013). Another point of consideration is with respect to divergence dating; recent advances in phylogenomics have greatly improved our ability to estimate evolutionary divergence times. However, because these datasets and methods have not been applied to all members of the focal clade, dates from previous studies are likely to be less precise and more error-prone. As a result, it is important to consider the sources for the dates being discussed within a comparative context and to make sure that comparisons being made are appropriate, particularly with respect to questions about evolutionary rates (Wheat and Wahlberg 2013).

2.3. Choosing appropriate levels of comparison

Inference of ancestral states is highly dependent on taxa examined and phenotypes assigned within a group. When mapping traits onto a phylogeny and searching for common signals, it is crucial to make sure the traits being examined are homologous rather than simply analogous. That is, the traits being compared should have a similar structural underpinning rather than being just superficially similar. This concept of ‘sameness’ can often be complicated, particularly with behavioral traits. One potential solution might be the development of an ontology of terms associated with social behavior so that definitions and suites of traits could be standardized across the field.

But at what level should these comparisons be made? One solution, taken in part by Cardinal and Danforth (2011), is to break ‘eusociality’ down into its constitutive parts in order to map ‘homologous’ behavioral units, such as overlapping generations, division of labor, caste differentiation, morphologically distinct gynes, progressive feeding, and swarming onto the phylogeny to study the origins and evolution of social behavior. Other approaches have grossly characterized behavior as solitary, primitive, or advanced eusocial (Figure 1). In both of these cases, the implicit assumption is that the mechanisms associated with the evolution of social behavior across independent origins (convergence) are the same. On the one hand, some might argue that the presence of a reproductive and a sterile worker caste is likely to be homologous across taxa. On the other hand, stating that ‘primitive eusociality’ in halictid bees and bumble bees is the same can be challenging because the social structures of these colonies can vary greatly. Instead, it may be a more likely assumption that ‘primitive eusociality’ evolves via some of the same evolutionary mechanisms across more closely related lineages (e.g., the two lineages of primitively eusocial halictids that have independently evolved eusociality; see Figure 1). Therefore, careful consideration of the focal

taxa and the behavioral traits being compared is critical to maximize the utility of the comparative approach. Future work could focus on mapping some of the aforementioned pre-adaptations onto the phylogeny along with other major life history traits such as progressive provisioning, extended parental care or swarming to determine if these traits are correlated with each other and/or with the evolution of eusociality as predicted.

3. OUTLOOK AND FUTURE DIRECTIONS

In recent years, the decreasing cost of next-generation sequencing and simultaneous explosion in the algorithms and software used to analyze huge volumes of data have made genomic technologies accessible to nearly any non-model organism. As a result, we are beginning to see a rapid increase in the number of social insect genomes that are available. If the sequenced taxa are chosen appropriately, whole genome sequences promise to be an invaluable key to unlock information on the factors associated with the evolution of social behavior. For example, within the halictids, eusociality has arisen independently two times and has been lost repeatedly, making this a particularly interesting group for comparative approaches. At least one halictid genome has been sequenced (*L. albipes*; Kocher et al. 2013), and with the addition of several other solitary and eusocial species, comparative ecological and genomic approaches can be easily employed. Within the Xylocopinae, there has only been a single origin of eusociality in the group, but there have been many subsequent losses, also creating a vast amount of variation in social behavior among closely related species that can be used to look for common factors associated with eusociality.

Socially polymorphic species that straddle the solitary–eusocial transition offer another insight into these mechanistic hypotheses (Wcislo and Danforth 1997; Schwarz et al. 2007). In some of these species, these behavioral differences appear to remain plastic. For example, in *H. rubicundus*, reciprocal transplant experiments have revealed

that most foundresses within these populations are capable of producing environmentally appropriate nesting behavior (e.g., solitary nests at higher latitudes and social nests at lower latitudes (Michener 1985; Field et al. 2010). Studies of *M. genalis* suggest that there is a fair amount of plasticity within this species as well, and that the social polymorphism results from size-based reproductive differences among foundresses (Kapheim et al. 2013). However, in other species or populations, the differences in social behavior appear to have a genetic underpinning. For example, in the North American populations of *H. rubicundus*, there are fixed genetic differences among social forms (Soucy and Danforth 2002). Likewise, in *L. albipes*, common garden experiments suggest a genetic underpinning of social phenotype (Plateaux-Quenu et al. 2000). Of the socially polymorphic Xylocopinae, behavioral variation is often associated with nest founding either as solitary or multiple females (e.g., *Ceratina australensis*, Rehan et al. 2010; *Xylocopa virginica*, Richards 2011). In all of these cases, the molecular genetic pathways underpinning differences in social behavior, whether fixed or plastic in their expression, remain to be determined. Further work characterizing behavioral variation, its degree of plasticity, and its genetic underpinning within these groups of species promises to greatly improve our understanding of sociality and its genetic basis.

4. CONCLUSIONS

The search for both proximate mechanisms and ultimate explanations associated with the evolution of social behavior is ongoing. Bees represent a particularly interesting group in which to examine them because the clade exhibits great variation in sociality. Eusociality has arisen four times independently within this group, with many subsequent modifications. This variation makes bees ideal for using comparative approaches to identify common factors associated with the gain and loss of social behavior. Furthermore, the well-resolved phylogeny within this monophyletic group

creates a robust statistical framework to which these analyses can be applied. However, careful examination of how sociality is defined and of the underlying assumptions created by choice of taxa will be critical to facilitate the success of these methods. Future work combining comparative ecological and genomic methods promises to illuminate our understanding of both how and why social behavior evolves.

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Des méthodes comparatives offrent des perspectives importantes dans la compréhension de l'évolution sociale chez les abeilles

Méthode comparative / évolution / organisation communautaire / semisocial / eusocial / génétique / génomique

Vergleichende Methoden ermöglichen eindrucksvolle Einblicke in die soziale Evolution von Bienen

vergleichende Methode / Evolution / kommunal / semisozial / eusozial / Genetik / Genomik

REFERENCES

- Alford, D.V. (1975) Bumblebees. Davis-Poynter, London
- Andersson, M. (1984) The Evolution of Eusociality. *Annu. Rev. Ecol. Syst.* **15**(IS), 165–189
- Avilés, L., Harwood, G. (2012) A quantitative index of sociality and its application to group-living spiders and other social organisms. *Ethology* **118**, 1219–1229
- Baglione, V., Canestrari, D., Marcos, J.M., Ekman, J. (2006) Experimentally increased food resources in the natal territory promote offspring philopatry and helping in cooperatively breeding carrion crows. *Proc. R. Soc. B: Biol. Sci.* **273**, 1529–1535

- Batra, S.W. (1966a) Nesting behavior of *Halictus scabiosae* in Switzerland (Hymenoptera:Halictidae). *Insectes Soc.* **13**, 87
- Batra, S.W.T. (1966b) Nest and social behavior of halictine bees of India. *Indian J. Entomol.* **28**, 375
- Biedermann, P., Taborsky, M. (2011) Larval helpers and age polyethism in ambrosia beetles. *Proc. Natl. Acad. Sci.* **108**(41), 17064–17069
- Bourke, A.F.G. (2011) *Principles of Social Evolution*. OUP Oxford
- Brady, S., Sipes, S., Pearson, A., Danforth, B. (2006) Recent and simultaneous origins of eusociality in halictid bees. *Proc. R. Soc. B* **273**, 1643–1649
- Breed, M. (1976) The evolution of social behavior in primitively social bees: a multivariate analysis. *Evolution* **30**, 234–240
- Bull, N.J., Schwarz, M.P. (1996) The habitat saturation hypothesis and sociality in an allodapine bee: cooperative nesting is not “making the best of a bad situation. *Behav. Ecol. Sociobiol.* **39**, 267–274
- Cardinal, S., Danforth, B.N. (2011) The antiquity and evolutionary history of social behavior in bees. *PLoS ONE* **6**, e21086. doi:10.1371/journal.pone.0021086
- Chenoweth, L.B., Tierney, S.M., Smith, J.A., et al. (2007) Social complexity in bees is not sufficient to explain lack of reversions to solitary living over long time scales. *BMC Evol. Biol.* **7**, 246. doi:10.1186/1471-2148-7-246
- Costa, J.T., Fitzgerald, T.D. (1996) Developments in social terminology: semantic battles in a conceptual war. *Trends Ecol. Evol.* **11**, 285
- Costa, J.T., Fitzgerald, T.D. (2005) Social terminology revisited: Where are we ten years later? **42**, 559–564
- Crespi, B.J., Yanega, D. (1995) The definition of eusociality. *Behav. Ecol.* **6**, 109–115
- Cronin, A.L., Hirata, M. (2003) Social polymorphism in the sweat bee *Lasioglossum (Evylaeus) baleicum* (Cockerell) (Hymenoptera, Halictidae) in Hokkaido, northern Japan. *Insectes Soc.* **50**, 379–386
- Danforth, B. (2007) Bees. *Curr Biol* **17**, R156–61. doi:10.1016/j.cub.2007.01.025
- Danforth, B.N., Cardinal, S., Praz, C., et al. (2013) The Impact of Molecular Data on Our Understanding of Bee Phylogeny and Evolution. *Annu. Rev. Entomol.* **58**, 57–78
- Davies, N.B., Krebs, J.R., West, S.A. (2012) *An Introduction to Behavioural Ecology*. In: Davies, N.B., Krebs, J.R., West, S.A. (eds.) Google Books, 4th edn. Blackwell Science Inc, West Sussex, UK
- Degnan, J.H., Rosenberg, N.A. (2008) Gene tree discordance, phylogenetic inference and the multi-species coalescent. *Trends Ecol. Evol.* **24**, 332–340
- Dew, R.M., Rehan, S.M., Tierney, S.M., et al. (2011) A single origin of large colony size in allodapine bees suggests a threshold event among 50 million years of evolutionary tinkering. *Insectes Soc.* **59**, 207–214
- Dornhaus, A., Chittka, L. (2001) Food alert in bumblebees (*Bombus terrestris*): possible mechanisms and evolutionary implications. *Behav. Ecol. Sociobiol.* **50**, 570–576
- Dornhaus, A., Brockmann, A., Chittka, L. (2003) Bumble bees alert to food with pheromone from tergal gland. *J. Comp. Physiol. A: Neuroethol., Sens., Neural, Behav. Physiol.* **189**, 47–51
- Eickwort, G.C., Eickwort, J.M., Gordon, J., Eickwort, M.A. (1996) Solitary behavior in a high-altitude population of the social sweat bee *Halictus rubicundus* (Hymenoptera: Halictidae). *Behav. Ecol. Sociobiol.* **38**, 227–233
- Emlen, S.T. (1982) The Evolution of Helping. I. An Ecological Constraints Model. *Am. Nat.* **119**, 29–39
- Evans, H.E. (1977) Extrinsic versus intrinsic factors in the evolution of insect sociality. *Bioscience* **27**, 613–617
- Faulkes, C.G., Bennett, N.C., Bruford, M.W., O'Brien, H.P., Aguilar, G.H., Jarvis, J.U.M. (1997) Ecological constraints drive social evolution in the African mole-rats. *Proc. R. Soc. B: Biological Sci.* **264**, 1619–1627
- Ferreira, P.G., Patalano, S., Chauhan, R., Ffrench-Constant, R., Gabaldon, T., Guigo, R., Sumner, S. (2013) Transcriptome analyses of primitively eusocial wasps reveal novel insights into the evolution of sociality and the origin of alternative phenotypes. *Genome Biol.* **14**, R20. doi:10.1186/gb-2013-14-2-r20
- Field, J. (1996) Patterns of provisioning and iteroparity in a solitary halictine bee, *Lasioglossum (Evylaeus) fratellum* (Perez), with notes on *L. (E.) calceatum* (Scop) and *L. (E.) villosulum* (K). *Insectes Soc.* **43**, 167
- Field, J., Shreeves, G., Sumner, S., Casiraghi, M. (2000) Insurance-based advantage to helpers in a tropical hover wasp. *Nature* **404**, 869–871
- Field, J., Paxton, R.J., Soro, A., Bridge, C. (2010) Cryptic plasticity underlies a major evolutionary transition. *Curr. Biol.* 1–4. doi:10.1016/j.cub.2010.10.020
- Field, J., Paxton, R.J., Soro, A., et al. (2012) Body size, demography and foraging in a socially plastic sweat bee: a common garden experiment. *Behav. Ecol. Sociobiol.* **66**, 743–756
- Fischman, B.J., Woodard, S.H., Robinson, G.E. (2011) Molecular evolutionary analyses of insect societies. *Proc Natl Acad Sci U S A* **108**(Suppl 2), 10847–10854
- Gadagkar, R. (1990) Evolution of eusociality: the advantage of assured fitness returns. *Philos. Trans. R. Soc. B: Biol. Sci.* **329**, 17–25
- Gadon, J., Helmkamp, M., Nygaard, S., Roux, J., Simola, D., Smith, C., Suen, G., Wurm, Y., Smith, C. (2012) The genomic impact of 100 million years of social evolution in seven ant species. *Trends Genet.* **28**, 14–21

- Garófalo, C.A. (1974) Aspectos evolutivos da biologia da reprodução em abelhas (Hymenoptera, Apoidea). Dissertation thesis. Universidade de São Paulo, Ribeirão Preto, Brazil
- Gibbs, J., Brady, S.G., Kanda, K., Danforth, B.N. (2012) Phylogeny of halictine bees supports a shared origin of eusociality for *Halictus* and *Lasioglossum* (Apoidea: Anthophila: Halictidae). *Mol. Phylogenet. Evol.* 1–14. doi:10.1016/j.ympev.2012.08.013
- Gillespie, J.H. (1977) Natural selection for variance in offspring numbers: a new evolutionary principle. *Am. Nat.* **111**, 1010–1014
- Goulson, D. (2003) Bumblebees: ecology and behaviour. Oxford University Press, Oxford
- Grafen, A. (1989) The Phylogenetic Regression. *Philos. Trans. R. Soc. Lond. Series B, Biol. Sci.* **326**, 119–157
- Hamilton, W.D. (1964) The genetical evolution of social behavior: I and II. *J. Theor. Biol.* **7**, 1
- Harvey, P.H., Pagel, M. (1991) The comparative method in evolutionary biology. Oxford University Press, Oxford
- Harvey, P.H., Kavanagh, M., Clutton-Brock, T.H. (1978) Sexual dimorphism in primate teeth. *J. Zoology* **186**, 475–485
- Heinrich, B. (1979) Bumblebee economics. Harvard University Press
- Hines, H., Hunt, J., O’Conner, T., Gillespie, J., Cameron, S.A. (2007) Multigene phylogeny reveals eusociality evolved twice in vespidae wasps. *Proc. Nat. Acad. Sci USA* **104**, 3295–3299
- Hoiss, B., Krauss, J., Potts, S.G., Roberts, S., Steffan-Dewenter, I. (2012) Altitude acts as an environmental filter on phylogenetic composition, traits and diversity in bee communities. *Proc. R. Soc. B: Biol. Sci.* **279**, 4447–4456
- Johnson, B.R., Borowiec, M.L., Chiu, J.C., Lee, E.K., Atallah, J., Ward, P.S. (2013) Phylogenomics resolves evolutionary relationships among ants, bees, and wasps. *Curr. Biol.* **23**(20), 2058–2062
- Kapheim, K.M., Smith, A.R., Nonacs, P., Weislo, W.T., Wayne, R.K. (2013) Foundress polyphenism and the origins of eusociality in a facultatively eusocial sweat bee, *Megalopta genalis* (Halictidae). *Behav. Ecol. Sociobiol.* **67**, 331–340
- Kaspari, M., Vargo, E.L. (1995) Colony size as a buffer against seasonality: Bergmann’s rule in social insects. *Am. Nat.* **145**, 610–632
- Keller, L., Perrin, N. (1995) Quantifying the level of eusociality. *Proc. R. Soc. B: Biol. Sci.* **260**, 311–315
- Kent, D.S., Simpson, J.A. (1992) Eusociality in the beetle *Austroplatypus incompertus* (Coleoptera: Curculionidae). *Naturwissenschaften* **79**, 86–87
- Knerer, G., Plateaux-Quenu, C. (1966) On polygyny in Halictinae (Hymenoptera). *C.R. hebd. Séances Acad. Sci. Série D: Sci. Nat* **263**, 2014–2017
- Kocher, S.D., Li, C., Yang W., Tan, H., Yi, S.V., Yang, X., Hoekstra, H.E., Zhang, G., Pierce, N.E., Yu, D.W. (2013) The genome of a socially polymorphic halictid bee, *Lasioglossum albipes*. *Genome. Biol.* **14**(12), R142
- Komdeur, J. (1992) Importance of habitat saturation and territory quality for evolution of cooperative breeding in the Seychelles warbler. *Nature* **358**, 494–495
- Lacey, E.A., Sherman, P.W. (2005) Redefining eusociality: concepts, goals and levels of analysis. *Ann. Zool. Fenn.* **42**, 573–577
- Langer, P., Hogendoorn, K., Keller, L. (2004) Tug-of-war over reproduction in a social bee. *Nature* **428**, 844–847
- Laverty, T.M., Plowright, R.C. (1985) Comparative bionomics of temperate and tropical bumble bees with special reference to *Bombus ephippiatus* (Hymenoptera: Apidae). *Can. Entomol.* **117**, 467–474
- Lin, N., Michener, C.D. (1972) Evolution of sociality in insects. *Q. Rev. Biol.* **47**, 131
- Lo, N., Gloag, R.S., Anderson, D.L., Oldroyd, B.P. (2010) A molecular phylogeny of the genus *Apis* suggests that the Giant Honey Bee of the Philippines, *A. breviligula* Maa, and the Plains Honey Bee of southern India, *A. indica* Fabricius, are valid species. *Syst. Entomol.* **35**, 226–233. doi:10.1111/j.1365-3113.2009.00504.x
- Maynard Smith, J., Szathmari, E. (1997) The major transitions in evolution. Oxford University Press, Oxford
- McLeish, M.J., Chapman, T.W. (2007) The origin of soldiers in the gall-inducing thrips of Australia (Thysanoptera: Phlaeothripidae). *Aust. J. Entomol.* **46**, 300–304
- Michener, C.D. (1969) Comparative social behavior of bees. *Annu. Rev. Entomol.* **14**, 299–342
- Michener, C.D. (1974) The Social Behavior of the Bees. Harvard University Press, Cambridge, MA
- Michener, C.D. (1985) From solitary to eusocial: Need there be a series of intervening species. *Exp. Behav. Ecol. Sociobiol.* **31**, 293
- Moreau, C.S., Bell, C.D., Vila, R., Archibald, S.B., Pierce, N.E. (2006) Phylogeny of the ants: diversification in the age of angiosperms. *Science* **312**, 101–104
- Murphy, C.M., Breed, M.D. (2007) A predictive distribution map for the giant tropical ant, *Paraponera clavata*. *J. Insect Sci.* **7**, 1–10
- Nonacs, P. (2000) Measuring and using skew in the study of social behavior and evolution. *Am. Nat.* **156**, 577–589
- Nowak, M.A., Tamita, C.E., Wilson, E.O. (2010) The evolution of eusociality. *Nature* **466**, 1057–1062
- O’Riain, M.J., Faulkes, C. (2008) African Mole-Rats: Eusociality, Relatedness and Ecological Constraints. In: Korb, J., Heinze, J. (eds.) *Ecology of Social Evolution*, pp. 207–223. Springer, Berlin
- Packer, L. (1990) Solitary and eusocial nests in a population of *Augochlorella striata* (Provancher) (Hymenoptera, Halictidae) at the northern edge of its range. *Behav. Ecol. Sociobiol.* **27**, 339–344

- Packer, L. (1991) The evolution of social behavior and nest architecture in sweat bees of the subgenus *Evyllaesus* (Hymenoptera : Halictidae): a phylogenetic approach. *Behav. Ecol. Sociobiol.* **29**, 153–160
- Packer, L., Knerer, G. (1985) Social evolution and its correlates in bees of the subgenus *Evyllaesus* (Hymenoptera: Halictidae). *Behav. Ecol. Sociobiol.* **27**, 339–344
- Pagel, M., Meade, A. (2006) Bayesian analysis of correlated evolution of discrete characters by reversible-jump Markov chain Monte Carlo. *Am. Nat.* **167**, 808–825
- Pagel, M., Meade, A. (2013) BayesTraits computer package, version 2.0. <http://www.evolution.rdg.ac.uk/BayesTraits.html>.
- Parker, J., Tsagkogeorga, G., Cotton, J.A., Liu, Y., Provero, P., Stupka, E., Rossiter, S. (2013) Genome-wide signatures of convergent evolution in echolocating mammals. *Nature* **502**, 228–231
- Paxton, R.J., Thoren, P.A., Tengo, J., Estoup, A., Pamilo, P. (1996) Mating structure and nestmate relatedness in a communal bee, *Andrena jacobii* (Hymenoptera, Andrenidae), using microsatellites. *Mol. Ecol.* **5**, 511–519
- Picker, M.D., Hoffman, M.T., Leverton, B. (2007) Density of *Microhodotermes viator* (Hodotermitidae) mounds in southern Africa in relation to rainfall and vegetative productivity gradients. *J. Zool.* **271**, 37–44
- Pike, N., Foster, W. (2008) The Ecology of Altruism in a Clonal Insect. In: Korb, J., Heinze, J. (eds.) *Ecology of Social Evolution*, pp. 37–56. Springer, Berlin
- Plateaux-Quenu, C. (1993a) Modalités de la socialisation chez les Halictinae (Hymenoptera, Halictidae). I: Biologie des Halictinae. *L'Année biologique* **32**(4), 183–204
- Plateaux-Quenu, C. (1993b) Flexibilité sociale chez *Evyllaesus albipes* (F.) (Hymenoptera, Halictinae). *Actes Coll Insectes Soc* **8**, 127–134
- Plateaux-Quenu, C., Plateaux, L., Packer, L. (2000) Population-typical behaviours are retained when eusocial and non-eusocial forms of *Evyllaesus albipes* (F.) (Hymenoptera, Halictidae) are reared simultaneously in the laboratory. *Insectes Soc* **47**, 263–270
- Purcell, J. (2011) Geographic patterns in the distribution of social systems in terrestrial arthropods. *Biol. Rev. Camb. Philos. Soc.* **86**, 475–491
- Rehan, S.M., Richards, M.H., Schwarz, M.P. (2009) Evidence of Social Nesting in the *Ceratina* of Borneo (Hymenoptera: Apidae). *J. Kansas Entomol. Soc.* **82**, 194–209
- Rehan, S.M., Richards, M.H., Schwarz, M.P. (2010) Social polymorphism in the Australian small carpenter bee, *Ceratina (Neoceratina) australensis*. *Insectes Soc.* **57**, 403–412
- Rehan, S.M., Leys, R., Schwarz, M.P. (2012) A mid-Cretaceous origin of sociality in xylocopine bees with only two origins of true worker castes indicates severe barriers to eusociality. *PLoS ONE* **7**, e34690. doi:10.1371/journal.pone.0034690
- Richards, M.H. (2011) Colony Social Organisation and Alternative Social Strategies in the Eastern Carpenter Bee, *Xylocopa virginica*. *J. Insect Behav.* **24**, 399–411
- Richards, M.H., Packer, L. (1996) The socioecology of body size variation in the primitively eusocial sweat bee, *Halictus ligatus* (Hymenoptera: Halictidae). *Oikos* **77**, 68–76
- Riechert, S.E., Roeloffs, R., Echternacht, A.C. (1986) The ecology of the cooperative spider *Agelena consociata* in Equatorial Africa (Araneae, Agelenidae). *J. Arachnol.* **14**, 175–191
- Rosenheim, J.A. (1990) Density-dependent parasitism and the evolution of aggregated nesting in the solitary Hymenoptera. *Ann. Entomol. Soc. Am.* **83**, 277–286
- Ross, K.G., Matthews, R.W. (1991) *The social biology of wasps*. Cornell University Press, Ithaca, New York
- Rubenstein, D.R., Lovette, I.J. (2007) Temporal environmental variability drives the evolution of cooperative breeding in birds. *Curr. Biol.* **17**, 1414–1419
- Sakagami, S.F., Munakata, M. (1972) Distribution and bionomics of a transpalaeartic eusocial halictine bee, *Lasioglossum (Evyllaesus) calceatum*, in northern Japan, with reference to its solitary life cycle at high altitude. *J. Fac. Sci. Hokkaido Univ. Ser. 6 Zoology.* **18**, 411
- Schwarz, M.P., Richards, M.H., Danforth, B.N. (2007) Changing paradigms in insect social evolution: insights from halictine and allodapine bees. *Annu. Rev. Entomol.* **52**, 127–150
- Schwarz, M.P., Tierney, S.M., Rehan, S.M., Chenoweth, L.B., Cooper, S.J.B. (2011) The evolution of eusociality in allodapine bees: workers began by waiting. *Biol. Lett.* **7**, 277–280
- Sherman, P.W., Lacey, E.A., Reeve, H.K., Keller, L. (1995) The eusociality continuum. *Behav. Ecol.* **6**, 102–108
- Smith, A.R., Wcislo, W.T., O'Donnell, S. (2003) Assured fitness returns favor sociality in a mass-provisioning sweat bee, *Megalopta genalis* (Hymenoptera: Halictidae). *Behav. Ecol. Sociobiol.* **54**, 14–21
- Smith, A.R., Kapheim, K.M., Pérez-Ortega, B., Brent, C.S., Wcislo, W.T. (2012) Juvenile hormone levels reflect social opportunities in the facultatively eusocial sweat bee *Megalopta genalis* (Hymenoptera: Halictidae). *Horm. Behav.* doi:10.1016/j.yhbeh.2012.08.012
- Song, S., Liu, L., Edwards, S.V. (2012) Resolving conflict in eutherian mammal phylogeny using phylogenomics and the multispecies coalescent model. *Proc. Natl Acad. Sci. USA* **109**, 14942–14947
- Soro, A., Field, J., Bridge, C., Cardinal, S.C., Paxton, R.J. (2010) Genetic differentiation across the social

- transition in a socially polymorphic sweat bee, *Halictus rubicundus*. *Mol. Ecol.* **19**, 3351–3363
- Soucy, S.L., Danforth, B.N. (2002) Phylogeography of the socially polymorphic sweat bee *Halictus rubicundus* (Hymenoptera: Halictidae). *Evolution* **56**, 330–341
- Spessa, A., Schwarz, M.P., Adams, M. (2000) Sociality in *Amphylaeus morosus* (Hymenoptera: Colletidae: Hylaeinae). *Ann. Entomol. Soc. Am.* **93**, 684–692
- Stacey, P.B., Ligon, J.D. (1991) The benefits-of-philopatry hypothesis for the evolution of cooperative breeding: variation in territory quality and group size effects. *Am. Nat.* **137**, 831–846
- Stark, R.E. (1992) Cooperative Nesting in the multivoltine large carpenter bee *Xylocopa sulcatipes* Maa (Apoidea: Anthophoridae): Do Helpers Gain or Lose to Solitary Females? *Ethology* **91**, 301–310
- Stevens, M.I., Hogendoorn, K., Schwarz, M.P. (2007) Evolution of sociality by natural selection on variances in reproductive fitness: evidence from a social bee. *BMC Evol. Biol.* **7**, 153
- Székely, T., Remeš, V., Freckleton, R.P., Liker, A. (2013) Why care? Inferring the evolution of complex social behaviour. *J. Evol. Biol.* **26**, 1381–1391
- Tierney, S.M., Smith, J.A., Chenoweth, L., Schwarz, M.P. (2008) Phylogenetics of allodapine bees: a review of social evolution, parasitism and biogeography. *Apidologie* **39**, 3–15
- Toth, A.L., Robinson, G.E. (2007) Evo-devo and the evolution of social behavior. *Trends Genet.* **23**, 334–341
- Toth, A.L., Varala, K., Newman, T.C., et al. (2007) Wasp gene expression supports an evolutionary link between maternal behavior and eusociality. *Science* **318**, 441–444
- Toth, A.L., Varala, K., Henshaw, M.T., Rodriguez-Zas, S.L., Hudson, M.E., Robinson, G.E. (2010) Brain transcriptomic analysis in paper wasps identifies genes associated with behaviour across social insect lineages. *Proc. R. Soc. B: Biol. Sci.* **277**, 2139–2148
- Ulrich, Y., Perrin, N., Chapuisat, M. (2009) Flexible social organization and high incidence of drifting in the sweat bee, *Halictus scabiosae*. *Mol. Ecol.* **18**, 1791–1800
- Vijay, N., Poelstra, J.W., Künstner, A., Wolf, J.B.W. (2013) Challenges and strategies in transcriptome assembly and differential gene expression quantification. A comprehensive in silico assessment of RNA-seq experiments. *Mol. Ecol.* **22**, 620–634
- Ware, J.L., Grimaldi, D.A., Engel, M.S. (2010) The effects of fossil placement and calibration on divergence times and rates: an example from the termites (Insecta: Isoptera). *Arthropod Struct. Dev.* **39**, 204–219. doi:10.1016/j.asd.2009.11.003
- Wcislo, W., Danforth, B. (1997) Secondarily solitary: the evolutionary loss of social behavior. *Trends Ecol. Evol.* **12**, 468–474
- Wcislo, W.T., Tierney, S.M. (2009) The evolution of communal behavior in bees and wasps: an alternative to eusociality. *Organization of Insect Societies: From Genome to Sociocomplexity* 148–169
- Wcislo, W.T., Arneson, L., Roesch, K., Gonzalez, V., Smith, A., Fernandez, H. (2004) The evolution of nocturnal behaviour in sweat bees, *Megalopta genalis* and *M. ecuadoria* (Hymenoptera: Halictidae): an escape from competitors and enemies? *Biol. J. Linn. Soc.* **83**, 377–387
- Wenzel, J.W., Pickering, J. (1991) Cooperative foraging, productivity, and the central limit theorem. *Proc. Natl Acad. Sci. U S A* **88**, 36–38
- West-Eberhard, M.J. (2003) *Developmental plasticity and evolution*. Oxford University Press
- Wheat, C.W., Wahlberg, N. (2013) Critiquing blind dating: the dangers of over-confident date estimates in comparative genomics. *Trends Ecol. Evol.* doi:10.1016/j.tree.2013.07.007
- Wilson, E.O. (1971) *The insect societies*. Harvard University Press, Cambridge
- Wilson, E.O. (1990) Success and dominance in ecosystems: the case of the social insects. Ohlendorf/Luhe, Germany
- Wilson, E.O., Holldobler, B. (2005) Eusociality: Origin and consequences. *Proc. Natl Acad. Sci. USA* **102**, 13367–13371
- Wong, J., Meunier, J., Kölliker, M. (2013) The evolution of parental care in insects. *Ecol. Entomol.* **38**, 123–137
- Woodard, S.H., Fischman, B.J., Venkat, A., Hudson, M.E., Varala, K., Cameron, S.A., Clark, A.G., Robinson, G.E. (2011) Genes involved in convergent evolution of eusociality in bees. *Proc. Natl Acad. Sci. USA* **108**, 7472–7477
- Yanega, D. (1988) Social plasticity and early-diapausing females in a primitively social bee. *Proc. Natl Acad. Sci. USA* **85**, 4374–4377
- Yang, Z., Bielawski, J.P. (2000) Statistical methods for detecting molecular adaptation. *Trends Ecol. Evol.* **15**, 496–503